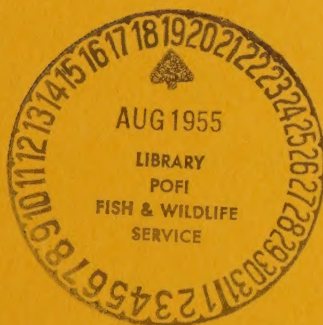


CONTRIBUTIONS
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For the Year 1954



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for the year 1954

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The Origin and Development of the Spermatophoric Mass of a Nephropsid Lobster, *Enoplometopus occidentalis* (Randall)¹

DONALD C. MATTHEWS²

INTRODUCTION

THE PURPOSE OF THIS PAPER on the origin and development of the spermatophoric mass of *Enoplometopus occidentalis* (Randall) is three-fold: (1) to increase our knowledge of the biology of this little-known species, (2) to show evidence in support of external fertilization, and (3) to extend the list of mechanically sperm-liberating families in Hawaii to include the Nephropsidae (Homaridae *auct.*, Nephropsidae *vide* Holthuis, 1946).

With the possible exception of the Cape crayfish (*Jasus lalandii*, von Bonde, 1936), all recorded observations indicate that the palinurids, the astacids, and the homarids produce continuous, highly convoluted spermatophoric tubes embedded in putty-like matrices (*Panulirus interruptus*—Allen, 1916; Fasten, 1917; Wilson, 1949; *P. argus*—Crawford and De Smidt, 1923; *P. penicillatus*—Matthews, 1951; *Potamobius troubridgii*—Andrews, 1931; *Homarus americanus*—Herrick, 1895).

Although the process has not been observed in every case, female pereopodal gouging of these spermatophores during oviposition probably allows the liberation of their spermatozoa and the subsequent external fertilization.

Among macruran spermatophores studied, mechanical liberation of sperm reaches its highest development in the scyllarid *Parribacus antarcticus* (Lund). The spermatophoric mass resembles that of the palinurids, the astacids, and the homarids, but certain of the pereopods are provided with special structures

for the mechanical liberation of the spermatozoa (Andrews, 1912; Matthews, 1953). Here, likewise, fertilization is probably external.

Although once obtainable from Honolulu markets (*vide* Rathbun, 1906: 900), *E. occidentalis* is now seldom seen here except at the Honolulu Aquarium, although it is occasionally taken on the reefs and at depths of a few fathoms (*vide* Edmondson, 1946: 257). Yet large numbers of *Enoplometopus* postlarvae found in the stomachs of the yellowfin tuna *Neothunnus macropterus* (Reintjes, unpubl. ms.) attest its prevalence in deeper water. Although only males were obtainable for dissection, a single female in the collection of the Bernice P. Bishop Museum was available for observation. This specimen was devoid of spermatophoric mass. The spermatophoric mass of *E. occidentalis* in so far as can be ascertained has not been investigated.

The writer wishes to thank Mr. Spencer Tinker, director of the Honolulu Aquarium, who furnished the living specimens.

METHODS AND TECHNIQUES

Mature male specimens of *E. occidentalis*, obtained from the Honolulu Aquarium in November, 1952, were used in this study. The reproductive organs were removed, fixed in either Bouin's or Zenker's fluid, dehydrated and cleared in dioxane, embedded in Tissuemat (54–56°C.), and sectioned at 10 microns. The mounted sections were stained with standard alumhaematoxylin and counterstained with eosin.

Certain vasa efferentia were placed in 0.1 N KOH. Others were dissected, the spermatophoric mass smeared on small glass plates, and these immersed in sea water.

¹ Contribution number 43, Hawaii Marine Laboratory. Manuscript received May 28, 1953.

² Department of Zoology and Entomology, University of Hawaii, Honolulu, Hawaii.

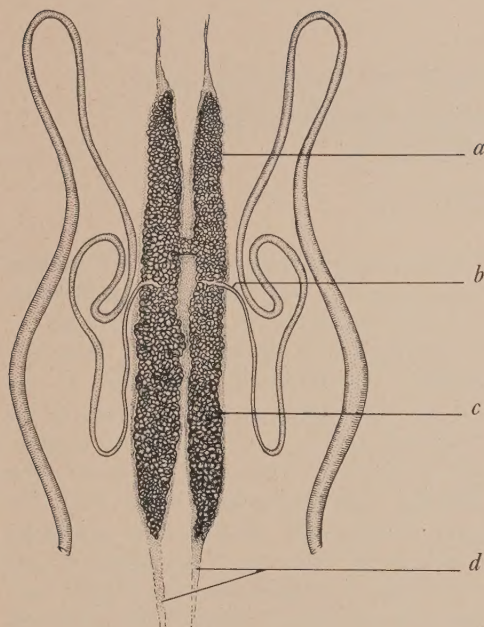


FIG. 1. Male reproductive system of *E. occidentalis* dissected to show: *a*, anterior region of testis; *b*, proximal portion of vas deferens; *c*, posterior region of testis; *d*, mesenteries. (2.5X)

RESULTS

Dissection of *E. occidentalis* reveals an H-shaped testicular mass (Fig. 1), the anterior portion of which (*a*) lies dorsal to the hepatopancreas and the posterior (*c*) contiguous with the digestive tract. The testes are held in place by mesenteries (*d*) and are abundantly supplied with blood vessels.

The slightly coiled vas deferens (Fig. 1*b*), which arises from the testis, increases in diameter distally and opens on the coxopodite of the fifth pereopod. The entire vas deferens is quiescent and, even when pinched with forceps, fails to eject its spermatophoric mass from the genital pore. There is no evidence of a hyaline line (*vide* Matthews, 1951).

In cross sections, follicles in all stages of maturity are seen throughout the testis. An immature follicle (Fig. 2) discloses large, primary spermatocytes (*c*), indistinguishable from the germinal epithelial cells (*a*) from

which they originate. Cells with indistinct cytoplasm but with strongly chromatophilic nuclei (*b*) appear scattered indiscriminately among the primary spermatocytes.

Cross sections of maturing follicles (Fig. 3) reveal that as the number of spermatids (*a*) increases, the number of primary spermatocytes (*b*) is reduced until ultimately a single, peripheral, germinal layer remains. The number of cells with strongly chromatophilic nuclei (*c*) also increases throughout the follicles.

Cross sections of mature follicles (Fig. 4) show the spermatids metamorphosed into spermatozoa (*a*) and an increase in the number of primary spermatocytes (*b*). The longitudinal sections of the collecting tubule (*c*) reveal that spermatozoa (*a*) which emanate from any one follicle remain in groups (*d*), and, although the cells with strongly chromatophilic nuclei (*e*) are numerous in the emptying follicle, they are seldom seen among the groups of spermatozoa in the tubule. A secretion (*f*) from the epithelial lining (*g*) of

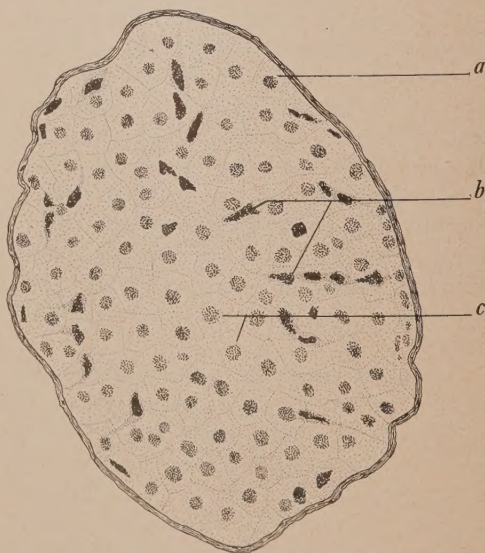


FIG. 2. Camera lucida drawing of a cross section through an immature follicle showing: *a*, germinal epithelium; *b*, nuclei of sustentacular cells; *c*, primary spermatocytes. (175X)

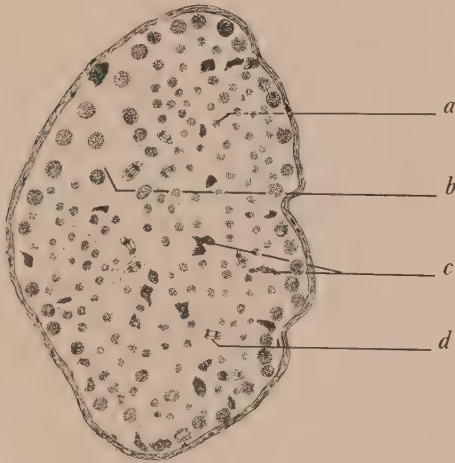


FIG. 3. Camera lucida drawing of a cross section through a follicle in the early stages of maturity showing: *a*, spermatids; *b*, primary spermatocytes; *c*, nuclei of sustentacular cells; *d*, meiotic figures of spermatid formation. (175 $\times$)

the tubule surrounds each group of spermatzoa.

Cross sections of the minute, proximal portion of the vas deferens (Fig. 5) reveal a tube in which the sperm mass (*a*) is surrounded by columnar epithelium (*b*) and a muscular layer (*c*). Although the columnar epithelial cells appear active, there is no evidence, in this region of the vas deferens, that a sheath is being formed around the sperm mass.

A portion of a cross section of the vas deferens (Fig. 6) (distad to the portion illustrated in Fig. 5) shows the sperm mass (*a*) enveloped by a spermatophoric sheath (*b*) and that this sheath is the product of the secretion from the epithelial cells (*c*). The thickness of the muscular layer (*d*) is only slightly increased over that illustrated in Figure 5.

Figure 7 illustrates a portion of a cross section through the distal region of the vas deferens. The sperm mass (*a*) is not only enveloped by a spermatophoric sheath (*b*), but a homogeneous matrix (*c*) is added by the epithelial cells (*e*). The matrix (*c*) is often separated from the epithelial cells (*e*) by a space (*d*). The muscular layer (*f*) is increased

in thickness and consists of longitudinal, diagonal, and circular fibers.

DISCUSSION

By mitotic division of the germinal epithelial cells (Fig. 2*a*), follicles fill with primary spermatocytes (*c*). During this process, certain cells with strongly chromatophilic nuclei (*b*) apparently arise from the germinal epithelial cells and occupy positions between the primary spermatocytes (*c*). Although mitotic figures are associated with the increase of primary spermatocytes, no mitotic figures accompany the increase of the strongly chromatophilic cells. Their method of multiplication remains obscure.

Concurrently, the primary spermatocytes (Fig. 3*b*) by two successive divisions (*d*) give



FIG. 4. Camera lucida drawing of cross section through mature follicles discharging their contents into the collecting tubule showing: *a*, spermatozoa; *b*, primary spermatocytes; *c*, longitudinal section of collecting tubule; *d*, groups of spermatozoa ejected from different follicles; *e*, contents of a single follicle being ejected into collecting tubule; *f*, secretion separating sperm groups; *g*, epithelial cells. (150 $\times$)

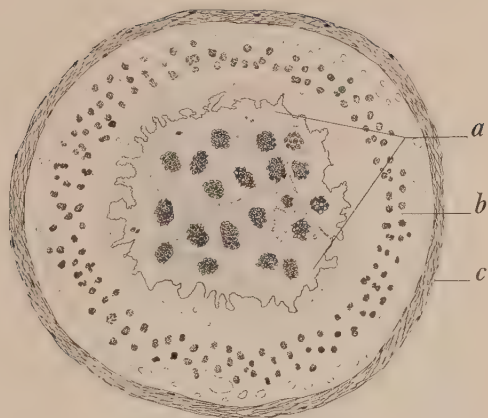


FIG. 5. Camera lucida drawing of a cross section through the minute, proximal portion of the vas deferens showing: *a*, sperm mass; *b*, columnar epithelium; *c*, muscle layer. (90 $\times$)

rise to spermatids (*a*) which later cluster about the cells with strongly chromatophilic nuclei (*c*). These are probably sustentacular cells (*c*) which serve the spermatids in their metamorphosis to spermatozoa.

Although most cross sections of the testis show mature follicles, few reveal the actual openings of these follicles into the collecting tubule; yet on these sections alone depends the understanding of the rhythmical nature of follicular activity. Concurrently with the metamorphosing of spermatids to spermatozoa (Fig. 4*a*), the germinal epithelium, by mitotic division, again produces primary spermatocytes (*b*) which fill the follicles and expel the spermatozoa (*a*). The sustentacular cells, once numerous among the metamorphosing spermatids (*e*), are difficult to observe in the extruded follicular contents. It is quite evident, however, that the many groups of spermatozoa (*d*) seen descending the collecting tubule (*c*) are each the entire extruded content of one single follicle and not, as previously reported for *Panulirus penicillatus* (Matthews, 1951) the result of the activity of sustentacular cells. These groups of spermatozoa are further separated by a secretion (*f*) from the epithelial lining (*g*) of the tubule. As previously men-

tioned, this secretion mixes freely between the groups of spermatozoa.

Cross sections of the minute, proximal portion of the vas deferens (Fig. 5) reveal that the sperm mass (*a*) has not yet acquired its sheath. However, the columnar epithelial cells (*b*) are extremely active, and their secretions may be identical with this structure (Fig. 6*b*) seen in more distal sections.

Less than one third of the vas deferens is traversed by the descending sperm mass (Fig. 5*a*) before it acquires its spermatophoric sheath (Fig. 6*b*). This sheath is the product of the secretion from epithelial cells (*c*) which, although shorter than those previously encountered, show little specialized arrangement. There are no deep folds or crypts (*vide* Matthews, 1951: 363, fig. 7). The epithelial cells bounding the lumen are arranged in a single cell layer, and their secretion envelopes the sperm mass forming the spermatophoric sheath.

Cross sections through the distal portion

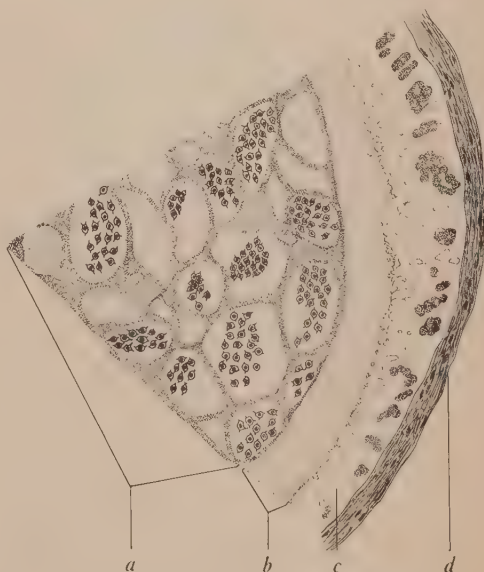


FIG. 6. Camera lucida drawing of a portion of a cross section of the vas deferens (distal to the portion illustrated in Fig. 5) showing: *a*, sperm mass; *b*, spermatophoric sheath; *c*, epithelial cells; *d*, muscle layer. (80 $\times$)



FIG. 7. Camera lucida drawing of a portion of a cross section of the distal region of the vas deferens showing: *a*, sperm mass; *b*, spermatophoric sheath; *c*, homogeneous matrix; *d*, space; *e*, epithelial cells; *f*, muscle layer. (90X)

of the vas deferens reveal what appears to be a sperm mass (Fig. 7*a*) surrounded by an extremely thick spermatophoric sheath (*b*, *c*). The reason for this misinterpretation lies in the fact that the sheath-forming secretion has the same consistency and staining properties as the matrix (Fig. 7*c*); both have an affinity for the cytoplasmic stain. Careful examination of the cross sections through this region, however, reveals a distinct diastem separating spermatophoric sheath (*b*) from matrix (*c*). Proof of the individual identity of these two secretions is further attested by placing the contents of the dissected, distal vas deferens in 0.1 N KOH. The outer matrix is readily soluble and soon disappears, whereas the inner spermatophoric wall, being less soluble, remains to disclose a highly coiled, continuous spermatophore.

The increased thickness of the muscular coat (Fig. 7*f*) probably plays a part in the expulsion of the spermatophoric mass during copulation; but whether it serves to segment the otherwise continuous spermatophoric tube into ampules is conjectural, since females with naturally occurring spermatophoric masses were not available for study. It seems very likely, however, that in either case the spermatozoa, encased in a spermatophoric sheath and enveloped in a hardened matrix, would

require a mechanical method for their liberation.

Further indirect evidence in support of external fertilization is obtained on examination of the female, for although a large seminal receptacle is present, it is found not to connect internally with the female reproductive system, and probably serves as a receptacle on which to receive the spermatophoric mass of the male.

Because this mass becomes hard in a few hours when experimentally placed on glass plates immersed in sea water, it appears reasonable to assume that in naturally formed spermatophoric masses of *E. occidentalis* a similar change in consistency would necessitate mechanical liberation of the spermatozoa.

SUMMARY

The male reproductive system of the homarid-like, nephropsid lobster *Enoplometopus occidentalis* (Randall) is dissected and figured.

Cross sections throughout the testis reveal follicles in various degrees of maturity. An immature follicle, by mitotic division of the cells of its germinal epithelium, becomes filled with primary spermatocytes. These cells, by both heterotypic and homeotypic divisions, form spermatids.

Concurrent with the formation of primary

spermatocytes and spermatids, certain cells containing strongly chromatophoric nuclei arise from the germinal epithelium and become widely dispersed throughout the follicle. These sustentacular cells probably aid the spermatids in their metamorphoses into spermatozoa.

Each group of spermatozoa seen in the collecting tubule is the extruded contents of a single follicle. This extrusion is caused by the production of a new group of primary spermatocytes filling the follicle. A secretion from the epithelial cells of the tubule surrounds each group of spermatozoa. As this material traverses the proximal portion of the vas deferens, a secretion from the undifferentiated epithelial cells surrounds the sperm mass and forms the spermatophoric sheath.

No typhlosole-like structure is present in the enlarged vas deferens, but epithelial cells secrete a matrix which envelops the spermatophoric sheath. That spermatophoric wall and matrix are distinct secretions is attested both by the diastem which separates them and by the greater solubility of the matrix in 0.1 N KOH.

Although neither naturally occurring spermatophores nor the process of fertilization was actually observed, the facts that the matrix hardens and that the seminal receptacle does not open internally strongly suggest mechanical liberation of the spermatozoa and subsequent external fertilization.

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New Records of Mysidacea and Euphausiacea from the Northeastern Pacific and Adjacent Areas¹

ALBERT H. BANNER²

SINCE THE PUBLICATION of my tripartite report on the Mysidacea and Euphausiacea of the northeastern Pacific (1948a, 1948b, 1950), some additional collections of these crustaceans from this region have been made available to me. These collections are in three groups: (1) specimens collected by the King Crab Investigation of the U. S. Fish and Wildlife Service in the eastern Bering Sea in 1941, principally from the stomachs of codfish and pollock; (2) specimens collected at the Arctic Research Laboratory at Point Barrow, Alaska, from 1948 to 1952, principally by G. E. MacGinitie and Ira L. Wiggins who were sponsored by research contracts from the Office of Naval Research to Johns Hopkins University and the California Institute of Technology; and (3) specimens collected by various persons, including myself, at random spots from Alaska to California after 1945. Many of the records are within the established range of the species, but even these are of importance because not much is known about these animals in the Pacific and, especially, in Alaskan waters. Some of the records below are extensions of the previously known ranges. Two new species are described, and a genus and several species previously described are placed in synonymy. In addition, lectotypes are designated for the species previously described by me (*op. cit.*) from this region.

To keep this paper as short as possible, rather than give the descriptions and full synonymy, reference will be made only to the original descriptions and to my previous

study or to the monograph of Tattersall (1951).

Boreomysis nobilis Sars

Boreomysis nobilis G. O. Sars, Arch. Math. Naturv. 4: 428, 1879.

——— Tattersall, U. S. Natl. Mus., Bul. 201: 47, 243, fig. 6, 1951.

SPECIMENS EXAMINED: *Arctic Research Laboratory*: No.?, Point Barrow, Alaska, Sept. 27, 1948; MacGinitie, collector. Four specimens. The largest specimen, an immature female, was 38 mm. long.

DISCUSSION: MacGinitie supplied the following notes: "Specimens collected near shore after several days of offshore wind followed by upwelling. [Body] translucent white with a red stripe (gut) down middle of back, a red stomach and mouth region. Eyes metallic crimson."

Previous records of this species have been confined to the subarctic Atlantic Ocean and the adjacent regions of the Arctic Ocean; it has been reported as far south as Newfoundland (Tattersall, 1939) and as far north as 77°N. on both coasts of Greenland (Stephensen, 1933, 1943). Its westernmost record until now was the western sounds leading into Baffin Bay (Tattersall, 1939).

Archaeomysis grebnitzkii Czerniavsky

Archaeomysis grebnitzkii Czerniavsky, St. Petersburg Nat., Trudy 12: 73, 1882; 18: pl. 30, figs. 17-24; pl. 32, figs. 19-20, 1887.

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¹ Contribution No. 45, Hawaii Marine Laboratory. Manuscript received March 11, 1953.

² Department of Zoology and Entomology, University of Hawaii.

Bul. 201: 81-86, figs. 21-22, 1951. [Redescribed.]

SPECIMENS EXAMINED: Numerous adult specimens of both sexes in sand in intertidal zone, Pismo Beach, Calif. (about 50 miles north of Point Conception), Nov., 1945; A. H. Banner, collector. The specimens were found burrowing in the sand in the wave-washed portion of the beach.

DISCUSSION: The specimens listed above and those previously examined and reported upon agree quite well with Tattersall's redescription and with his criteria for the separation of *A. maculata* (Holmes) from *A. grebnitzkii*. However, in both groups of specimens the posterior dorsal tooth of the fifth abdominal segment was present, a characteristic Tattersall reported to be unique to *A. maculata*. Therefore, reliance should not be placed upon that to separate the two species.

My previous records for the species reached only to the southern portion of the state of Washington, and those of Tattersall reached only to Half Moon Bay, immediately south of San Francisco, California; the present record, therefore, is the most southerly for the species. It is noteworthy that, during the month in which this collection was made at Pismo Beach, many other beaches to the south, especially in the Los Angeles area, were investigated and neither *A. grebnitzkii* nor *A. maculata* were found.

Mysis oculata (Fabricius)

Cancer oculatus Fabricius, Fauna Groenlandica, pp. 245-246, 1780.

Pugetomysis litoralis Banner, Roy. Canad. Inst., Trans. 27: 105, pl. 6, figs. 18a-k, 1948.

Mysis oculata Tattersall, U. S. Natl. Mus., Bul. 201: 165-167, fig. 61, 1951. [Redescribed.]

SPECIMENS EXAMINED: *Arctic Research Laboratory*: No. 492, washed ashore near Point Barrow, Alaska, Sept. 22, 1949; MacGinitie, collector. One immature female.

No. 659, plankton tow off Point Barrow, Alaska, Oct. 31, 1949; MacGinitie, collector.

About 20 specimens, immature males and females, mature females.

No. 660, plankton tow off Point Barrow, Alaska, in churning water, evening, Sept. 1, 1949; MacGinitie, collector. Four immature males and females.

No.?, plankton tow off Point Barrow, Alaska, July 23, 1948; MacGinitie, collector. Ten larval forms.

No. 489, beach, Point Barrow, Alaska, July 24, 1950; Wiggins, collector. Five immature males and females.

Red Station 2. Dredged at 70°08'N., 143°-54'W., 1 specimen.

Red Station 3. Dredged at 70°03'N., 145°-14'W., approximately 150 specimens.

Red Station 4. Dredged at 70°12'N., 145°-55'W., 6 specimens.

Red Station 5. Dredged at 70°11'N., 146°-15'W., 177 specimens.

Red Station 6. Dredged at 70°15'N., 146°-50'W., approximately 150 specimens.

Red Station 7. Dredged at 70°26'N., 147°-55'W., approximately 100 specimens.

Red Station 8. Dredged at 70°31'N., 148°-50'W., 26 specimens.

Red Station 10. Dredged at 70°34'N., 150°-15'W., approximately 100 specimens.

Red Station 11. Dredged at 70°43'N., 150°-59'W., approximately 100 specimens.

Red Station 12. Dredged at 70°40'N., 151°-50'W., 17 specimens.

Red Station 15. Dredged at 70°57'N., 153°-15'W., 1 specimen.

Red Station 16. Dredged at 70°57'N., 154°-16'W., 5 specimens.

Red Station 18. Dredged at 71°13'N., 155°-48'W., 15 specimens.

The stations of the "Red" were taken between August 9 and 12, 1953. The depths varied from 9 to 42 feet; the surface temperatures from 2.6°C. to 4.8°C.; the bottom temperatures from -3.5°C. to 3.2°C.; the surface salinity from 8.87 o/oo to 23.48 o/oo; the bottom salinity from 24.33 o/oo to 30.61 o/oo; the bottoms were of mud, sand, gravel,

and clay. Further details on the stations may be found in Wilimovsky (1953).

DISCUSSION: Specimens apparently of this species are represented in the collection only by mature females and immature specimens of both sexes. The immature males are about 10 millimeters long, whereas the two mature females are over 20 millimeters long. The specimens agree well with the described characteristics of *M. oculata*, except that the pleopods of the males are obviously immature.

In these males all pleopods save the fourth are uniramous, and in the fourth the exopod is divided into only three articles, whereas the endopod has no subdivisions. However, in adult *M. oculata* both the third and fourth pleopods are biramous, the third with an exopod of five articles and the fourth with an exopod of seven articles. Because of the close similarity of these specimens to the descriptions of *M. oculata*, and because of the much greater size of the mature females, it was decided that the males were immature.

This condition is the same as that of the immature males described by me as *Pugetomysis litoralis*. I had presumed from the fourth pleopods of these specimens that they were almost mature. Since examining the Point Barrow specimens, I have re-examined the specimens in the type lot, and I can find no differences that could be considered of major importance. Therefore, *P. litoralis* is a synonym of *M. oculata*, and the genus *Pugetomysis*, erected to contain only that species, is a synonym. As a consequence, the type will not be deposited in the U. S. National Museum.

Mysis oculata is circumpolar in distribution and has been reported from the arctic coasts of North America, Europe, and Asia; it has been reported from the Arctic Ocean on either side of Bering Straits and as far south as Kiska, Alaska.

The specimens originally reported as *P. litoralis* came from Friday Harbor, Washington, and represent the first record of the species in the Pacific Ocean proper and the first

record of the genus or species along the western coast of subtemperate and temperate North America.

Mysis relicta Lovén

Mysis relicta Lovén, Svenska Vetensk. Akad., Öfversigt af . . . förhandl., p. 285, 1862.

——— Tattersall, U. S. Natl. Mus., Bul. 201: 167–168, fig. 62, 1951.

SPECIMENS EXAMINED: *Arctic Research Laboratory*: No. 489, beach, Point Barrow, Alaska, Sept. 24, 1950; Wiggins, collector. Two specimens, immature.

No. 665, plankton tow off Point Barrow, Alaska, Sept. 30, 1949; MacGinitie, collector. About 500 specimens, immature.

No.?, Elson Lagoon near Point Barrow, Alaska, Sept. 1, 1949; MacGinitie, collector. About 50 specimens, immature.

No.?, Elson Lagoon near Point Barrow, Alaska, July 28, 1950; MacGinitie, collector. Five specimens, immature.

No.?, Nuwuk Pond near Point Barrow, Alaska, Aug., 1952 (chlorinity 1.3 o/oo); John Mohr, collector. Twelve specimens, immature.

DISCUSSION: *Mysis relicta* is distinguished from the very closely related *M. oculata* chiefly by a more shallow and more pointed indentation on the posterior margin of the telson and a broader squame of the second antenna. However, these conditions are found in the larval form of *M. oculata* as well. In view of the work of Olafsson (1918) which indicated that *M. relicta* might not be produced by any inherited differences from the stem form but merely by the lesser salinity of their environment, I am not personally convinced of the validity of the species. However, until more definite information is available I will accept the decision of previous workers that *M. relicta* is a separate and valid species.

The telsons of the specimens listed are almost identical to those described for *M. relicta*, but the antennal squame is more like that of *M. oculata*, almost six times as long as

broad. Because of the small size and the sexual immaturity of these specimens they possibly could be interpreted as young *M. oculata*. However, inasmuch as the cleft of the telson in specimens of *M. oculata* of similar size had the adult configuration, the present specimens were considered to be young of *M. relicta*.

Like *M. oculata*, *M. relicta* is circumpolar in distribution and occurs not only in brackish and fresh water lying near the present Arctic Ocean but also as far south as the lakes left by the continental ice sheets, such as the Great Lakes of North America. Dr. Mohr, in a personal communication, has described the pond where he collected these specimens at Point Barrow:

There extends northeast from Pt. Barrow base for about seven miles a peninsula . . . called Nuwuk. On the tip there are several shallow pools and a larger one roughly a block long and at least 17 feet deep near the center. . . . Nuwuk pond is possibly a hundred yards from the present seashore. Between the main pond and the sea is a smaller pond which would about halve that distance, and very clear and apparently quite recent channels connect the smaller to the main pond. . . . I had the strong impression that Nuwuk Pond was of recent separation from the sea. I think [that the geologists of the party were inclined to agree with this].

This species has been reported previously from Arctic Alaska.

*Neomysis rayi*³ (Murdock)

Mysis rayii Murdock, U. S. Natl. Mus., Proc. 7: 519, 1885.

Neomysis rayii Banner, Roy. Canad. Acad., Trans. 27: 78-82, pl. 2, fig. 12, 1948.

Neomysis rayii Tattersall, U. S. Natl. Mus., Bul. 201: 181-186, figs. 68-71, 1951.

SPECIMENS EXAMINED: *Arctic Research Laboratory*: No. 532, beach, Point Barrow, Alaska, Sept. 28, 1950; Wiggins, collector. One specimen.

³ The terminal "i" must be dropped from this patronymic according to the International Rules of Zoological Nomenclature as amended in Paris in 1948—see Bul. Zool. Nomen. 4: 68, 1950.

No.?, plankton tow near shore, July 13, 1950; MacGinitie, collector. One specimen, broken (identification not certain).

King Crab Investigation: No. C-109, stomach of *Gadus macrocephalus*, Point Moller, Alaska, 20-23 fathoms, June 5, 1941. One mature male 32 mm. long.

DISCUSSION: These records add nothing to the known range, as Point Barrow is the type locality and the species have been previously reported from the Bering Sea region.

Neomysis kadiakensis Ortmann

Neomysis kadiakensis Ortmann, U. S. Natl. Mus., Proc. 34: 8, 1908.

——— Banner, Roy. Canad. Inst., Trans. 27: 83, pl. 3, fig. 13, 1948.

——— Tattersall, U. S. Natl. Mus., Bul. 201: 192-194, fig. 75, 1951.

SPECIMENS EXAMINED: *King Crab Investigation*: No. C-87, Akutan Bay, Alaska, April 27, 1941. Three specimens.

DISCUSSION: These specimens are from slightly west of the previous northern and western record, that of Ortmann for the type specimens from Kodiak Island, Alaska.

Neomysis awatschensis (Brandt)

Fig. 1

Mysis awatschensis Brandt, Middendorf's Reise . . . 2(1): 126, 1851.

Neomysis awatschensis Zimmer, Fauna Arctica, 3: 468, 1904.

Neomysis nigra Nakazawa, Annot. Zool. Japonensis 7(4): 248, 1910.

Heteromysis intermedia Czerniavsky, St. Petersburg Nat., Trudy 13: 35, 1882.

Neomysis intermedia Zimmer, Fauna Arctica 3: 469, 1904.

Neomysis isaza Marukawa, Annot. Oceanog. Rech. 2: 6, 1928.

Neomysis mercedis Holmes, Calif. Acad. Sci., Proc. II, 6: 199, 1897.

[For a full listing of all citations to these nominal species, see Tattersall, 1951: 187-191.]

SPECIMENS EXAMINED: Naknek River, Alaskan Peninsula (Bristol Bay, approximately 59°N., 157°W.), low tide, near shore, July 11, 1946; Chester R. Mattson, collector; specimens loaned by Dr. J. E. Lynch, University of Washington. About 50 specimens.

DISCUSSION: The animals of this complex, described as five different species and more recently resolved to three species (*N. awatschensis*, *N. intermedia*, and *N. mercedis*), are known to extend around the rim of the North Pacific from San Francisco, California, to the coasts of Japan and China. *N. mercedis* reached from San Francisco Bay to the waters of southern British Columbia; *N. intermedia* from south central Alaska and Bering Island to the coasts of Siberia, Japan, and China; and *N. awatschensis* was known only from Kamchatka (Tattersall, 1951: 190, in his distributional lists forgot to mention the type locality, Awatscha Bay in Kamchatka), Japan, and China. All are known to inhabit brackish water, and in Washington, at least, *N. mercedis* penetrates into fresh-water lakes (Banner, 1948b: 75).

These three forms, accepted as separate species, have been known to be closely related. Tattersall in 1932 (p. 321) and again in 1951 (p. 187 *et seq.*) remarks upon this but gives criteria by which the species may be separated. The specimens listed above from the Bering Sea were somewhat intermediate in some of these criteria and have caused me to consider again, on the basis of the variations observed in specimens from Washington and Alaska, the validity of the separation of the three species.

Tattersall's criteria for the separation of the three species are listed below, together with notes on the specimens from Washington and Alaska.

Size: Tattersall states that mature *N. awatschensis* are 10 millimeters long, whereas *N. mercedis* are 15 millimeters long. However, some mature specimens from Washington known as *N. mercedis* are 11 millimeters long. The size of *N. intermedia* was not given by

Tattersall, but specimens from Alaska approaching that species are 10 millimeters long and mature.

Color: Tattersall states that *N. awatschensis* is black and *N. mercedis* "is certainly not black." Observations on living specimens originally identified as *N. mercedis*, both those collected so recently as to have the color unchanged and those kept alive in aquaria, have not shown any jet-black individuals, but the color was found to range from almost transparent to a condition where the chromatophores were sufficiently expanded to make the individual almost black. In aquaria it was found that the color of the individuals changed with their environment. Several specimens were found that were pale green in color. This variability in the color pattern was reminiscent of *Acanthomysis sculpta* (Tattersall), which was found to vary from transparent, through sandy (and green), to jet black. To my knowledge there are no color notes on *N. intermedia*.

Rostral plate: *N. mercedis* is supposed to have a quadrangular rostral plate, *N. intermedia* a rounded rostral plate, and *N. awatschensis* a pointed rostral plate. The forms from Washington and from Alaska show variation in this plate, with only a few showing even an approximation of the quadrilateral condition and the rest varying from broadly rounded to narrowly rounded. In none was the rostrum pointed; however, those in which the tip was narrowly rounded certainly approached the pointed condition.

Antennal squame: This is supposed to be 8 times as long as broad in *N. mercedis* and *N. awatschensis* but 10 times as long as broad in *N. intermedia*. In some of the specimens from Washington the squames are slightly longer than 8 times as long as broad, while in many of the specimens from Bristol Bay the squames are about 9 times as long as broad.

Eyes: In *N. mercedis* and *N. intermedia* the entire eyestalk is 1.5 times as long as the cornea is broad, with the cornea occupying less than 0.5 the length of the entire stalk

and with the breadth of the peduncle equal to 0.4 of its length. In *N. awatschensis* the entire eyestalk is slightly less than 1.5 times as long as the cornea is broad, with the cornea occupying 0.5 the length of the entire stalk, and the peduncle is 0.5 as wide as the stalk is long. The specimens examined agree with *N. mercedis* and *N. intermedia*.

Thoracic endopods: Tattersall reports that the sixth joint of the thoracic endopods is divided into 8–10 secondary joints in *N. mercedis*, into 7–11 joints in *N. intermedia*, and into 6–8 joints in *N. awatschensis*. Smaller specimens of *N. mercedis* from Washington have 6–8 joints, whereas the larger have 8–10; specimens from Alaska approaching *N. intermedia* have 7–10 joints.

Fourth pleopods of the males: In *N. mercedis* and *N. awatschensis* the terminal article of the outer branch of the fourth pleopods of the males is supposed to be 0.25 the length of the proximal joint and definitely shorter than the terminal setae, whereas in *N. intermedia* the terminal article is 0.5 the length of the proximal and longer than the setae. However, in mature specimens from Washington the terminal article is 0.3 to 0.2 the length of the proximal, whereas immature specimens have the proportions given for *N. intermedia*.

Telson: Tattersall reports the telson to be similar in *N. mercedis* and *N. intermedia*, being twice as long as broad, the apex 0.2 the breadth of the base and the lateral spines shorter than the spaces between their bases; the only difference is that in *N. mercedis* there are 15 lateral spines (as shown by Tattersall in fig. 72), whereas in *N. intermedia* there are 13–21 lateral spines. He reports that the telson of *N. awatschensis* is 1.75 times as long as broad, the apex is 0.25 the breadth of the base, and the posterior of the 17–21 lateral spines are longer than the spaces between their bases. In the specimens from fresh water from Washington the tip of the telson is about 0.12 the breadth of the base, but in some of the more brackish-water specimens from Washington and Alaska the tip is 0.25 to 0.2

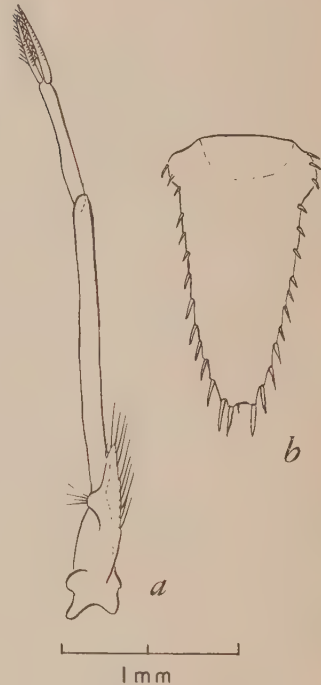


FIG. 1. *Neomysis awatschensis* (Brandt), specimen from Naknek River, Alaska. *a*, Fourth pleopod of male; *b*, telson, showing extreme condition of the spines. (Both drawings to the same scale.)

the breadth of the base. The number and length of the lateral spines are also variable, even those from the same locality; for example, some of those from Naknek River had spines longer than the spaces between their bases, therefore more like *N. awatschensis*, whereas in others the spines were shorter, like the other two species. The length-breadth relationship showed similar variation.

With this summation it can be seen that the three species were separated by rather small differences, but such differences, were they to remain constant, would have been adequate for the separation of the species. However, the specimens examined showed all these characteristics to be variable beyond the limits set for the separation of the three species. The sole exception may be found in the rather slight differences reported for the eyes, and

on the closely related *N. rayi* (Murdock) this was shown to be an unreliable characteristic. Probably the most firm of the criteria might be found in the shape of the rostral plate and the fourth pleopods of the male. However, it was precisely these characteristics again that were found to be without worth in the attempted separation of *N. rayi* from *N. franciscorum*. In fact, the differences in this complex parallel the differences found between the warm-water *N. franciscorum* (as it was previously known) and the colder-water *N. rayi*.

Unfortunately, the collections do not permit the complete removal of all differences, but when it is considered that there are stretches of the coast of the North Pacific hundreds of miles long where the species must exist but where no collections have ever been made, it is logical to presume that complete intergradations between the various types could be found.

It is for these reasons that *N. mercedis* and *N. intermedia* have been placed in synonymy to *N. awatschensis*.

Acanthomysis pseudomacropsis (Tattersall)

Neomysis pseudomacropsis Tattersall, Contrib. Canad. Biol. 8: 94-97, figs. 7a-b, 8a-f, 1933.

Acanthomysis pseudomacropsis Banner, Roy. Canad. Inst., Trans. 27: 89, 1948.

——— Tattersall, U. S. Natl. Mus., Bul. 200: 217, figs. 91, 92, 1951.

SPECIMENS EXAMINED: *King Crab Investigation*: No. C-109, stomachs of *Gadus macrocephalus*, Point Moller, Alaska, May 6, 1941. Two specimens from separate stomachs.

No. C-117, stomach of *Theragra chalcogramma*, Cape Seniavin, Alaska, May 8, 1941. Twenty specimens.

DISCUSSION: Previous records of this species have extended from Washington to the coast of Siberia; these records, therefore, do not extend the range.

Acanthomysis sculpta (Tattersall)

Neomysis sculpta Tattersall, Contrib. Canad. Biol. 8: 197-200, figs. 9a-b, 10a-d, 11a-b, 1933.

Acanthomysis sculpta Banner, Roy. Canad. Inst., Trans. 27: 97-99, 1948.

——— Tattersall, U. S. Natl. Mus., Bul. 201: 248, 1951.

SPECIMENS EXAMINED: Fifteen specimens from Pismo Beach, California (about 50 miles north of Point Conception), from the sand in the intertidal zone, Nov., 1946; A. H. Banner, collector.

DISCUSSION: As this species is known from Vancouver Island, Canada, to La Jolla, California, this record merely fills in part of the range.

Acanthomysis alaskensis n. sp.

Fig. 2

DESCRIPTION: Rostrum triangular, acute, with tip reaching almost to the proximal portion of cornea of eye; dorsal surface straight in profile. Anterolateral corners of carapace produced and acute.

Eyes large, with peduncle short and heavy, broader than long. Inner superior surface of peduncle with poorly developed triangular papilla. Cornea expanded, dorsoventrally compressed and subovate in lateral view.

Antennular peduncle showing usual sexual dimorphism, in males with distal article heavier than in females and bearing well-developed *process masculinus*. Basicerite of antenna bearing a small but acute tooth. Antennal peduncle reaching only to middle of last article of antennular peduncle. Squame twice as long as antennular peduncle, six times as long as broad; distal twentieth demarked by feeble articulation.

Labrum with acute anterior process.

Protopodite of first thoracic leg laterally expanded so that exopod and endopod are some distance removed from each other, and bearing well-developed, lobe-like endite. Pro-podi of third to eighth thoracic legs with 6

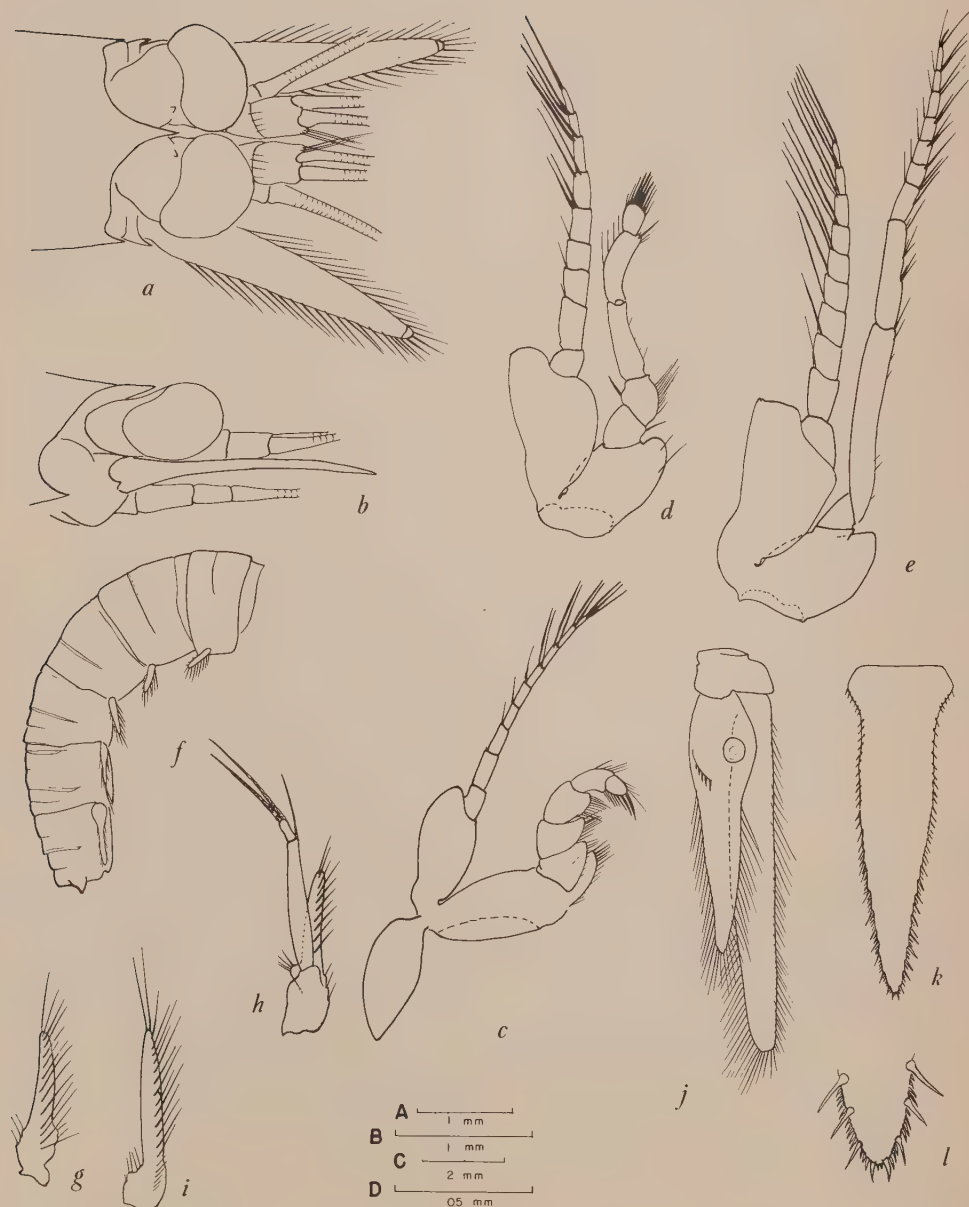


FIG. 2. *Acanthomysis alaskensis*, n. sp. *a*, Anterior region, dorsal aspect; *b*, anterior region, lateral aspect; *c*, first thoracic leg; *d*, second thoracic leg; *e*, seventh thoracic leg; *f*, abdomen, lateral aspect; *g*, third pleopod, male; *h*, fourth pleopod, male; *i*, fifth pleopod, male; *j*, uropod; *k*, telson; *l*, tip of telson. All drawings except *g*, *b*, and *i* from a mature female. (*a*, *b*, *j*, *k*, scale A; *c*, *d*, *e*, *g*, *h*, *i*, scale B; *f*, scale C; *l*, scale D.)

to 8 secondary articulations. Armature of basal plate of exopod variable.

Terga of first five abdominal somites bearing transverse folds somewhat similar to those described for *Acanthomysis davis* Banner (1948b: 96). Sixth abdominal segment with three folds that are discontinuous dorsally; anterior pair set on a slight angle to transverse line of body and poorly developed; posterior two pairs transverse to body and well developed.

Telson slightly over twice as long as the sixth abdominal segment, triangular in shape with anterior lateral margins concave, middle and posterior lateral margins straight to slightly convex. Telson 3 times as long as broad at base, with breadth at tip one-twentieth breadth of base. Spines on basal half of lateral margins more or less regularly placed and of subequal lengths; larger spines of posterior half of lateral margins separated from each other by groups of 3 to 5 much shorter spines; penultimate lateral spines with tips reaching beyond tip of telson; final spines very slightly longer than tip is broad and separated by 2 very short spines.

Inner uropod reaching almost to end of telson and bearing 4 to 5 spines near statocyst; outer uropod 1.5 times length of inner.

Only fourth pleopods of male biramous, with tip of exopod reaching slightly beyond end of fifth abdominal segment. Proximal article of exopod 4.5 times length of distal and bearing a single strong spine; distal article bearing 2 strong spines that are 4 times length of distal article. Fifth pleopod of males 0.8 as long as fourth.

SPECIMENS EXAMINED: Type specimen: A submature male, 19.7 mm. long, collected by the King Crab Investigation, haul C-117, June 8, 1941, from the stomach of *Theragra chalcogramma* (Pallas) (Alaskan pollock), taken off Cape Seniavin on the Alaskan Peninsula (about 160°W.) in 23–26 fathoms. U. S. National Museum 95638.

Paratypes: Many others collected with type, some in semidigested condition. Five others also collected by the King Crab Investigation

at Point Moller, Alaska, from the stomachs of cod.

DISCUSSION: These specimens were interpreted to be immature on the basis of characteristics of the female, not the male, for the females of size similar to the type did not have their oostegites fully developed. On the other hand, it may be that the males are mature but reach a smaller size at maturity than do the females.

This species belongs to the group in this genus that have the abdomens with dorsal folds in the chitin: *A. mitsukurii* (Nakazawa) (1910: 250), *A. stelleri* (Derzhavin) (1913: 202), *A. davis* Banner (1949: 95), *A. costata* (Holmes) (1900: 221), *A. sculpta* (Tattersall) (1933: 197), and *A. borealis* (described in this paper). *A. mitsukurii* can be distinguished from this species and from all other species in the group by the presence of small denticles on the folds of the abdomen, as well as by other characteristics. *A. sculpta* can be distinguished by the presence of four large spines on the tip of the telson and by the lack of a strong bristle on the basal article of the exopod of the fourth pleopods of the male. *A. borealis* is easily separated by the rounded tip of the telson and by the uniform series of spines on its distal tenth.

However, this species and the remaining three species, *A. costata*, *A. stelleri*, and *A. davis*, are most obviously closely related. *A. costata* and *A. davis* are both smaller species found in more southern waters, whereas *A. stelleri* and *A. alaskensis* are larger northern forms. The characteristics that will serve to separate them are given in Table 1.

From the examination of this table it will be seen that the species have much in common and that the diagnostic characteristics—primarily the rostrum, eyes, antennal squame, abdominal grooves, shape, and armature of the telson—are small differences in proportions in parts that are known in other species to be variable. The fourth pleopods of the male show less difference than is found between the northern and southern races of *Neomysis rayi*.

TABLE 1
CHARACTERISTICS WHICH DIFFERENTIATE THE SPECIES IN THE *Acanthomysis costata* GROUP

CHARACTERISTIC	<i>A. alaskensis</i>	<i>A. stelleri</i> *	<i>A. costata</i> †	<i>A. davis</i>
Size.....	About 20 mm.	About 20 mm.	8 mm.	9-11 mm.
Rostrum.....	Acute; reaching almost to end of ocular peduncle	Not as acute as <i>A. alaskensis</i> ; reaching to middle of ocular peduncle	"short . . . pointed"	Subacute; not reaching to middle of ocular peduncle
Cornea.....	Dorsoventrally compressed; laterally broadened	Rounded (?)	Rounded (?)	Rounded to slightly compressed; not markedly laterally broadened
Antennal squame....	7 times as long as broad; 2 times length of antennular peduncle	7 times as long as broad; 1.5 times length of antennular peduncle	5 times as long as broad; 1.3 times length of antennular peduncle	5 times as long as broad; 1.3 times length of antennular peduncle
Propodi of thoracic legs 3-8.....	6-8 secondary articles	4-6 secondary articles	4-5 secondary articles	4-5 secondary articles
Rugae of abdominal somites				
1.....	1 fold	2 folds, discontinuous dorsally	3 folds	2 folds, 1st slight
2.....	1 fold	2 folds, discontinuous dorsally	2 folds	2 folds, 1st slight
3.....	1 fold	3 folds, discontinuous dorsally	2 folds	2 folds, 1st slight
4.....	3 folds	2 folds, discontinuous dorsally	2 folds	3 folds
5.....	3 folds, 2 discontinuous dorsally	2 folds, 1 discontinuous dorsally	2 folds	3 folds, 2 discontinuous dorsally
6.....	3 folds, all discontinuous dorsally	1 fold, continuous dorsally	2 folds, first projecting as triangular plate, second continuous	3 folds, all discontinuous dorsally
Telson				
length/length 6th abdominal segment	2/1	1.5/1	2/1	2/1
length/breadth at base.....	3/1	2.5/1	2.5/1	2.5/1
breadth at tip/				
breadth at base....	1/20	1/6	1/15	1/40
penultimate long lateral spines.....	Reaching beyond tip of telson	Reaching beyond tip of telson	Not reaching to tip of telson	Reaching about mid-length of telson
posterolateral spines	Length equal to breadth of telson tip	Length equal to breadth of telson tip	Length equal to twice breadth of telson tip	Telson tip so different that comparison not valid
4th pleopods of male exopod				
basal article.....	4.5 times length distal article	Undescribed	5 times length distal article	4.5 times length distal article
terminal setae.....	4 times length distal article	Undescribed	3 times length distal article	3 times length distal article

* Comparison based on Derzhavin's figures and short description; the telson shown by Tattersall (1951: 212, fig. 88) does not agree with that shown for the type species.

† Comparison based on Holmes's original description (1900: 221) and upon the more adequate redescription by Tattersall (1932: 327). The specimen depicted by Hansen (1913: 177) showed a telson with the terminal spines like *A. sculpia* (Tattersall), not *A. costata*.

With the geographic variation of *Neomysis rayi* and *N. awatschensis*, members of a closely related genus, in mind and viewing the relatively minor differences between the species of the *Acanthomysis costata* group, I am of the opinion that this complex, too, may represent only a single species with various geographic races. However, as I have been able to find no variation in those specimens that I have studied nor have variations been reported by workers from other of these species, and as the characteristics as they are now given are sufficient to separate the four forms, I have decided for the time to maintain them as four species.

Acanthomysis borealis n. sp.

Fig. 3

Acanthomysis sp. Banner, Roy. Canad. Inst., Trans. 27: 101–102, pl. 6, figs. 17a–d, 1949.

DESCRIPTION: Anterolateral corners of the carapace produced and acute. Rostrum triangular with acute tip reaching only to basal portion of ocular peduncle.

Eyes similar to those of *A. sculpta* (Tattersall), 1.3 times as long as broad; corneas occupying distal 0.4, subhemispherical. Peduncle with very short dorsal papilla.

Antennular peduncle 1.5 times length of eyes, slender, with first article slightly less than twice as long as broad. Basicerite of antenna with small but acute tooth; peduncle reaching only to end of first antennular article; squame 7 times as long as broad, with distal 0.04 separated by usual articulation.

Labrum with acute anterior process. Mouthparts usual.

Endopods of third to eighth thoracic legs with 5–7 secondary articulations in propodi; dactyli about 0.5 the diameter and length of distal propodal article. Basal plates of exopods with or without denticle.

Abdomen with following grooves and folds:

Segment 1: single fold in middle; two rounded grooves;

Segment 2: single fold in middle; posterior

groove poorly defined;

Segment 3: same as segment 2;

Segment 4: single fold in middle; posterior groove better defined;

Segment 5: heavy rounded ridge in middle, discontinuous over midline and projecting on either side of midline as rounded lobes; posterior to middle ridge a heavy fold, almost discontinuous over midline; near posterior margin another rounded ridge and groove, also discontinuous; posterior margin projecting over base of segment 6 as rounded lobe;

Segment 6: similar to segment 5, except ridges and folds are heavier and discontinuous over midline.

Telson 1.8 times length of sixth abdominal segment, 3.5 times as long as broad. Lateral margins anteriorly convex for short distance, then concave, convex again in middle, and in posterior half slightly concave. Tip so narrowly truncate and meeting rounded lateral margins at such an angle that it at first appears rounded. Spines of anterior half of lateral margins subequal in length; those from middle to near tip alternating between longer spines and groups of 2–6 shorter spines; in posterior tenth spines again subequal in length and 0.5 to 0.66 length of long spines in preceding portion. Posterolateral spines of tip slightly longer than lateral spines adjacent; median terminal spines 0.5 length of posterolateral spines.

Inner uropod 0.7 length of outer, slightly shorter than telson and bearing four spines near statocyst.

SPECIMENS EXAMINED: Type specimen: A mature female 19 mm. long collected from the stomach of a cod by the U. S. Fish and Wildlife King Crab Investigation, No. C-108, off Port Moller, Bristol Bay, Alaska, in 20–22 fathoms, May 6, 1941. U. S. National Museum 95639.

Paratype: an immature female, 15.5 mm. long, same data as type.

DISCUSSION: These specimens agree well with the specimen from Olga Bay, Kodiak

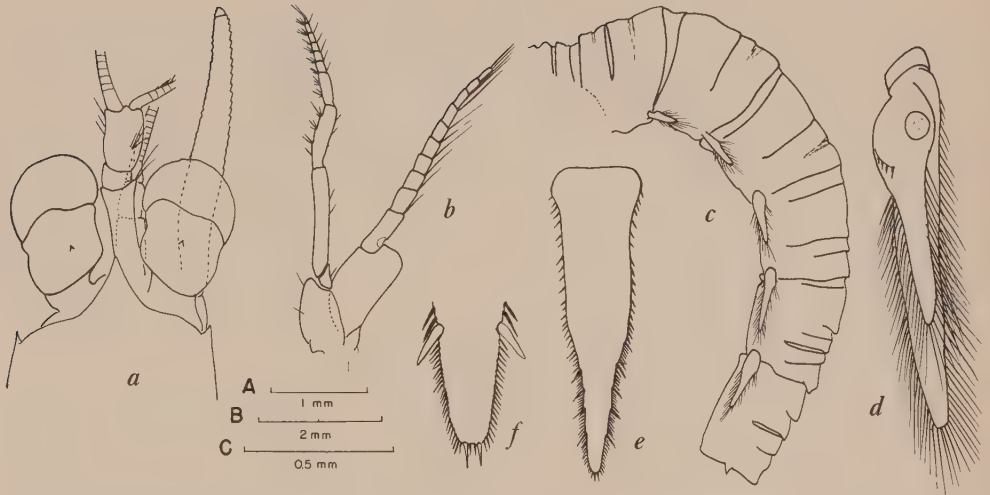


FIG. 3. *Acanthomysis borealis*, n. sp. *a*, Anterior region, dorsal aspect; *b*, sixth thoracic leg; *c*, abdomen, lateral view; *d*, uropod (statocyst spines are on other side of inner uropod); *e*, telson; *f*, tip of telson. (*a*, *b*, *d*, *e*, scale A; *c*, scale B; *f*, scale C.)

Island, Alaska, described by me as *Acanthomysis* sp. in 1949. (In the description of this species [p. 102] there is a typographical error: the telson is 1.7 mm. long instead of 0.7 mm. long.) There are slight differences in proportions as, for example, those of the eyes, squame, and telson; the dorsal papilla of the ocular peduncle was not observed previously; and there are slight differences in the rugae and folds of the abdomen. But as the general configurations are similar and the distal end of the telsons are almost identical, and as the Kodiak specimen is markedly immature, the differences are not considered to be enough to warrant separation of the two forms.

The Kodiak specimen was left unnamed, as it was felt that without mature specimens too much faith should not be placed in its characteristics. This specimen shows that the distinguishing characteristics, especially the telson, are not influenced by growth. It is unfortunate that there are no mature males available, but the unique telson should be adequate to separate this species from related species, whether male or female specimens are examined.

As discussed under *A. alaskensis*, there are now seven species in the genus *Acanthomysis* with rugose abdomens. Some of the characteristics of those species are discussed under *A. alaskensis*; here it will suffice to say that all other members of the group have plainly truncate telsons with relatively straight sides immediately proximal to the truncation and that in all of them the posterolateral spines of the telson are markedly larger than the spines immediately adjacent on the lateral margins. In this species, on the other hand, the posterior margin of the telson is so indecisively truncate that it appears rounded, and the posterolateral spines are only slightly larger than the adjacent spines. Other characteristics can be used to supplement these differences—the large medial spines found on the tip of the telson in *A. sculpta*, the dorso-ventrally compressed eye in *A. alaskensis*, etc. (see Table 1).

Thysanoessa raschi (M. Sars)

Thysanopoda raschii M. Sars, Vidensk. Selsk. Christiania, Forhandl., 1863, p. 83.

Thysanoessa raschii Banner, Roy. Canad. Inst., Trans. 28: 27, pl. 3, figs. 22a–b, 1950. [Includes synonymy.]

SPECIMENS EXAMINED: *Arctic Research Laboratory*: No. 341, plankton tow off Point Barrow, July 25, 1948; MacGinitie, collector. Four specimens.

No. 482, washed ashore near Point Barrow, Sept. 20, 1949; MacGinitie, collector. Six specimens.

No. 661, same as No. 482, Sept. 20, 1949. One specimen.

No.?, plankton tow near Point Barrow, Alaska, 1:30 P.M., Oct. 31, 1949; MacGinitie, collector. One specimen.

No.?, from gullet of Sabine gull, Elson Lagoon, Point Barrow, Alaska, Oct. 31, 1949; MacGinitie, collector. One specimen.

No. 489, Point Barrow Base, Alaska, July 24, 1950; Wiggins, collector. Eight specimens.

King Crab Investigation: C-108, C-109, Point Moller, Alaska, May 6, 1941, thousands of specimens from the stomachs of about 15 cod (*Gadus macrocephalus*) each on two separate samplings. Some of the cod had between 500 and 1,000 euphausiids in their stomachs.

C-117, C-119, Cape Seniavin, Alaska, May 8, 9, 1941, less than 1,000 specimens from one pollock (*Theragra chalcogramma*) and three cod stomachs.

DISCUSSION: The specimens listed are within the previously known range. It is notable that no other euphausiid was found in the cod and pollock stomachs. This is similar to the role *Thysanoessa inermis* (Krøyer) played in the food of the 23 whales from Akutan (Banner, 1950: 27). The difference in food may be due to the fact that *T. raschii* is an inshore species, whereas *T. inermis* is more commonly found beyond the margin of the continental shelf.

Thysanoessa longipes Brandt

Thysanoessa longipes Brandt, Middendorff's Reise . . . 2(1): 128, pl. 6, figs. 1–4, 1851.

————— Banner, Roy. Canad. Inst., Trans. 28: 21, 1950.

SPECIMENS EXAMINED: *Arctic Research Laboratory*: No. 662, washed ashore, Point Barrow, Sept. 26, 1949; MacGinitie, collector. One specimen.

No. 663, same data as above, Sept. 27, 1949. About 25 specimens, all immature.

No.?, same data as above, July 20, 1950. Two specimens.

DISCUSSION: This species was known previously from the Point Barrow region on the basis of only two specimens reported by Schmitt (1919: 8b).

Thysanoessa inermis (Krøyer)

Thysanopoda inermis Krøyer, 'Gaimard's Reise, pl. 7, fig. 2a, 1846.

Thysanoessa inermis Banner, Roy. Canad. Inst., Trans. 28: 24, pl. 3, figs. 23a–b, 1950. [Includes synonymy.]

SPECIMENS EXAMINED: *Arctic Research Laboratory*: No.?, along shore, Point Barrow Base, July 20, 1950; MacGinitie, collector. One specimen.

No.?, gullet, Sabine gull, Elson Lagoon, Point Barrow, Aug. 26, 1950; MacGinitie, collector. Three or four specimens, fragmentary.

No. 489, beach at Point Barrow Base, July 24, 1950; Wiggins, collector. One specimen.

DISCUSSION: This species also was reported from the Point Barrow region by Schmitt (1919: 8b).

TYPE MATERIAL OF PREVIOUSLY DESCRIBED SPECIES

In my previous study of mysids and euphausiids from this region, I published names and descriptions of a number of new species for which I did not designate any particular specimen as the type for the species. The type specimens have now been selected from the series that were used in drawing up the descriptions (lectotypes, therefore, from a co-

typic series) and have been deposited in the United States National Museum. The following is the pertinent information about these types.

MYSIDACEA

Boreomysis kincaidi Banner (1948a: 362). International Fisheries Commission haul 2005c, 51°15'N., 130°25'W., 700, 800, 900 M., Mar. 19, 1941. U. S. N. M. 95627.

Euchaetomeropsis pacifica Banner (1948a: 386). International Fisheries Commission haul 1911a, 51°00'N., 130°00'W., 100, 200, 300 M., Dec. 31, 1940. U. S. N. M. 95628.

Caesaromysis vancleveii Banner (1948a: 389). Type (male): International Fisheries Commission haul 22b, 58°59'N., 150°58'W., 150, 250 M., Jan. 30, 1928. U. S. N. M. 95629.

Allotype (female): International Fisheries Commission haul 1267c, 52°00'N., 130°24'W., 700, 800, 900 M., Jan. 7, 1935. U. S. N. M. 95630.

Acanthomysis nephrophthalma Banner (1948b: 93). Type (male): International Fisheries Commission haul 1284c, 53°47'N., 134°02'W., 700, 800 M., Jan. 10, 1935. U. S. N. M. 95631.

Allotype (female): Same as type. U. S. N. M. 95632.

Acanthomysis davisii Banner (1948b: 95). Type (male): Friday Harbor, Washington, surface waters near shore, Aug. 2, 1937, collected by Charles C. Davis. U. S. N. M. 95633.

Allotype (female): Same as type. U. S. N. M. 95634.

Acanthomysis sculpta (Tattersall) var. *nuda* Banner (1948b: 100). Makah Bay, Washington, shallow water near beach, Sept. 4, 1940, collected by A. H. Banner. (Note: this is not a subspecies but the designation of an infrasubspecific entity.) U. S. N. M. 95635.

Mysidella americana Banner (1948b: 109). International Fisheries Commission haul 1935b, 52°00'N., 131°14'W., 500, 600 M.

(net hit bottom), Jan. 13, 1941. U. S. N. M. 95636.

EUPHAUSIACEA

Thysanopoda dubia Banner (1950: 9). International Fisheries Commission haul 1997a, 51°41'N., 131°02'W., 100, 200, 300 M., Feb. 17, 1941. U. S. N. M. 95637.

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Observations on the Oxygen Consumption of Certain Marine Crustacea¹

P. B. VAN WEEL, JOHN E. RANDALL, AND M. TAKATA²

MANY PAPERS dealing with the respiration of Crustacea with respect to ecological problems have appeared (Bull, 1931; Edwards and Irving, 1943; van Heerdt, 1940; van Heerdt and Krijgsman, 1939; Hyman, 1932; Johnson, 1936; Munro Fox and Simmonds, 1933; Munro Fox and Johnson, 1933, 1934; Peters, 1935; Raffy, 1934; Thienemann, 1928), but a number of these seem to give results of dubious validity. The oxygen consumption has been measured under different conditions of temperature, oxygen tension, etc. More recently the effect of carbon dioxide on the oxygen consumption has also been studied (Johnson, 1936; van Heerdt, 1940; van Heerdt and Krijgsman, 1939; Schlieper and Peters, 1937; Segaar, 1941). However, comparative studies using the same method and technique on a number of Crustacea from different habitats are rare, although the results of such investigations would have a positive bearing on ecological and comparative physiological problems. It is well known that many animals, living in a special habitat, may show a distinct physiological adaptation to that habitat. Therefore, the oxygen consumption, at varying oxygen tensions, was studied in a number of Crustacea from different and specific habitats.

MATERIALS AND METHOD

The following species were selected: *Metopograpsus messor* Forskål, a crab which appar-

ently lives for the most part out of the water; *Pseudozius castrus* Adams and White, which lives underneath rocks in the tidal zone; *Phymodius unguatus* Milne Edwards and *Platypodia granulosa* Rüppell, which are found in abundance between branches of coral; *Pseudosquilla ciliata* Miers and *Calappa hepatica* Linn., which live on and in sandy flats rather devoid of organic matter (as compared with muddy flats); *Podophthalmus vigil* Fabricius, a swimming crab found in large numbers on and in muddy flats rich in organic matter.

To determine the oxygen consumption at different tensions, each animal was placed in a glass tube 20 centimeters long and with an inner diameter of 26 millimeters. This tube was closed with rubber stoppers through which were inserted a glass inlet tube at one end, and an outlet tube and a thermometer at the other end. Water, containing a known quantity of oxygen in solution, flowed from a carboy through the tubes. An overflow, which gave a constant head of pressure, and screw clamps adjusted the flow and kept it at a constant rate of 50 cubic centimeters per minute (3 liters per hour). Care was taken that no air bubbles remained in the whole system. Samples of 125 cubic centimeters were taken from the in- and outflowing water (5 minutes "overflow time" was allowed to prevent errors caused by absorption of oxygen from the air) and immediately titrated (Winckler method) to determine the quantity of oxygen present. The animals were left in the flowing water for at least 30 minutes before a sample was taken, whenever water of different oxygen content was used. Control experiments showed that this period of time

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² Professor of Zoology and graduate students, respectively, in the Department of Zoology and Entomology, University of Hawaii, Honolulu, Hawaii.

was sufficient to equilibrate the oxygen consumption in the new medium. This method also precluded the possibility of an accumulation of excretions which might affect the results of the Winkler titration.

The animals could move in their containers, but usually they very soon became inactive and quiet. However, inasmuch as they were not artificially immobilized and did move now and then, certain fluctuations did appear in the oxygen consumption. This condition was included because it is known (Jordan and Guittart, 1938) that artificial immobilization markedly affects the rate of oxygen consumption. The results of experiments with animals, which for some reason or other remained restless, were discarded because their oxygen consumption was very irregular, as could be expected.

The percentage of oxygen in the water in the carboy was varied by bubbling nitrogen through it for varying periods of time or by adding normal sea water to oxygen-deficient water. As the present investigation was concerned with the effect of varying oxygen tensions on the oxygen consumption at normal temperatures and as no method of maintaining the temperature at a constant room temperature was available, no special provisions were made to keep the temperature at a constant level throughout all experiments. However, the large carboys (5-gallon capacity) insured a comparatively constant temperature during a whole experiment, the greatest difference encountered being 0.5°C. between start and finish.

Several attempts were made to count the number of beats per minute of the scaphognathites and pleopods. At the normal high temperature their movements were so quick and the rhythm often so irregular (especially at lower oxygen tensions) that it was impossible to obtain satisfactory counts. However, it was sometimes possible to observe an increase or decrease of the rate of the beats.

Prior to each experiment the animals were starved for 24 hours.

EXPERIMENTS

The results of the determinations of the oxygen content of in- and outflowing water are presented in Table 1, which also includes the weight of each animal and the temperature of the water. The percentage of oxygen consumed by the animals as a function of oxygen present in the inflowing water has been computed.

TABLE 1

THE PERCENTAGE OF OXYGEN CONSUMED FROM FLOWING WATER OF VARIED OXYGEN CONCENTRATION BY SEVERAL SPECIES OF CRUSTACEA

SPECIES	CC. OF O ₂ PER LITER		PERCENTAGE OF OXYGEN CONSUMED
	Inflow	Outflow	
<i>Pseudozoea caystrus</i>	6.24	6.08	2.6
Weight	6.24	6.06	2.9
3 grams	6.09	5.93	2.6
Temperature	5.28	5.18	1.9
27.5-27.8°C.	4.38	4.26	2.7
	4.38	4.23	3.4
	4.38	4.20	4.1
	2.88	2.83	1.7
	2.88	2.84	1.4
	2.59	2.42	6.6
	2.17	1.99	8.3
	1.67	1.57	6.0
	1.67	1.57	6.0
	1.27	1.18	7.1
	1.27	1.14	10.2
	1.21	1.11	8.3
	1.18	1.13	4.2
	1.18	1.13	4.2
Weight	6.18	6.01	2.8
2.9 grams	6.12	5.97	2.5
Temperature	6.12	5.98	2.6
26.6-27.0°C.	5.61	5.50	2.3
	4.40	4.31	2.1
	4.40	4.29	2.5
	3.83	3.76	1.9
	3.51	3.46	1.4
	2.90	2.86	1.4
	2.63	2.48	5.7
	2.08	1.93	7.0
	1.80	1.66	7.8
	1.59	1.46	8.2
	1.31	1.19	9.1
	1.31	1.20	8.5
	1.12	1.08	3.6
	1.12	1.07	4.5
	1.12	1.07	4.5

TABLE 1 (Continued)

SPECIES	CC. OF O ₂ PER LITER		PERCENTAGE OF OXYGEN CONSUMED
	Inflow	Outflow	
<i>Metopograpsus messor</i>	6.24	6.03	3.4
Weight	6.24	6.08	2.6
5.9 grams	5.71	5.62	1.6
Temperature	5.71	5.64	1.2
27.5–27.8°C.	5.28	5.16	2.3
	5.28	5.19	1.7
	4.38	4.18	4.5
	4.38	4.21	3.9
	3.91	3.79	3.1
	3.91	3.82	2.3
	2.88	2.81	2.4
	2.88	2.78	3.4
	2.59	2.40	7.3
	2.59	2.45	5.4
	2.17	1.93	11.1
	2.17	1.98	8.8
	1.27	1.10	13.4
	1.27	1.09	15.7
	1.21	1.07	11.6
	1.21	1.09	9.9
	1.18	1.06	10.2
	1.18	1.07	9.3
	0.96	0.93	3.1
Weight	6.18	6.01	2.8
6.2 grams	6.12	5.97	2.5
Temperature	6.12	5.94	2.9
26.6–27.0°C.	5.61	5.50	2.0
	4.40	4.29	2.5
	4.40	4.25	3.4
	3.83	3.70	3.4
	3.51	3.40	3.1
	2.90	2.81	2.8
	2.63	2.57	2.3
	2.08	1.92	7.7
	1.80	1.60	11.1
	1.59	1.40	12.0
	1.31	1.16	11.4
	1.31	1.16	11.4
	1.12	1.03	8.0
	1.12	1.05	6.3
	1.12	1.06	5.4
<i>Calappa hepatica</i>	4.19	3.57	14.8
Weight	4.19	3.57	14.8
7.9 grams	4.17	3.64	12.7
Temperature	4.17	3.49	16.3
26.0–26.2°C.	4.15	3.80	8.4
	4.14	3.73	9.9
	4.14	3.73	9.9
	4.14	3.71	10.4
	4.09	3.73	8.8
	3.68	3.24	12.0
	3.68	3.16	14.0
	3.49	3.10	11.3
	3.39	2.87	15.3

TABLE 1 (Continued)

SPECIES	CC. OF O ₂ PER LITER		PERCENTAGE OF OXYGEN CONSUMED
	Inflow	Outflow	
	3.30	2.81	14.8
	3.28	2.73	16.8
	3.18	2.80	12.0
	2.99	2.52	15.7
	2.75	2.33	15.3
	2.69	2.33	13.4
	2.61	2.19	16.1
	2.58	2.24	13.2
	2.20	1.76	20.1
	1.98	1.55	21.7
	1.83	1.37	25.1
	1.59	1.22	23.3
	1.54	1.19	22.7
	1.45	1.05	27.6
	1.35	0.98	27.4
	1.31	1.01	22.9
	1.19	1.00	16.0
Weight	4.23	3.64	13.9
6.8 grams	4.23	3.68	13.0
Temperature	4.10	3.48	15.1
26.1–26.4°C.	4.08	3.48	14.7
	3.53	3.11	11.9
	3.20	2.84	11.3
	2.61	2.15	17.6
	2.20	1.78	19.1
	2.18	1.73	20.6
	2.18	1.72	21.1
	1.91	1.47	22.0
	1.80	1.37	23.9
	1.80	1.36	24.4
	1.37	1.03	24.9
	1.37	1.05	23.4
	1.37	1.03	24.9
	1.14	0.98	14.0
<i>Pseudosquilla ciliata</i>	4.19	3.86	7.9
Weight	4.19	3.86	7.9
4.7 grams	4.17	3.87	7.2
Temperature	4.15	4.02	3.1
26.0–26.2°C.	4.14	3.95	4.6
	4.14	4.05	2.2
	4.14	4.07	1.7
	4.09	3.85	5.9
	3.68	3.56	3.3
	3.50	3.33	5.0
	3.28	3.22	2.4
	2.99	2.89	3.3
	2.75	2.64	4.0
	2.74	2.57	6.2
	2.73	2.61	4.4
	2.69	2.53	5.9
	2.61	2.48	3.1
	2.58	2.42	5.9
	2.20	1.97	10.3
	2.00	1.77	11.5

TABLE 1 (Continued)

SPECIES	CC. OF O ₂ PER LITER		PERCENTAGE OF OXYGEN CONSUMED
	Inflow	Outflow	
	1.98	1.71	13.9
	1.59	1.36	14.5
	1.45	1.27	12.4
	1.31	1.15	12.2
<i>Phymodius unguatus</i>	4.53	3.75	17.2
Weight	4.53	3.89	14.1
12.5 grams	3.46	3.12	9.8
Temperature	3.12	2.90	7.1
26.8°C.	2.98	2.86	4.0
	2.93	2.59	11.6
	2.93	2.55	13.0
	2.66	2.33	12.4
	2.46	2.03	17.5
	2.35	1.78	24.3
	1.78	1.28	28.1
	1.50	1.30	13.3
	1.34	1.16	13.4
Weight	4.56	3.92	14.0
11.9 grams	4.41	3.77	14.5
Temperature	3.59	3.23	10.0
26.5-26.8°C.	3.59	3.26	9.2
	2.92	2.51	14.0
	2.71	2.35	13.3
	2.60	2.26	13.0
	2.38	1.92	19.3
	2.33	1.85	20.6
	1.85	1.52	17.8
	1.61	1.38	14.3
	1.61	1.39	13.7
	1.28	1.11	13.3
<i>Platypodia granulosa</i>	4.53	3.57	21.2
Weight	4.53	3.42	24.5
6.0 grams	3.46	2.88	16.8
Temperature	3.12	2.58	17.3
26.8°C.	2.98	2.57	13.8
	2.93	2.40	18.1
	2.93	2.53	13.7
	2.66	2.14	19.5
	2.53	2.18	13.8
	2.46	2.05	16.7
	2.35	1.72	26.8
	1.78	1.35	24.2
	1.50	1.14	24.0
	1.34	0.98	26.9
Weight	4.56	3.48	23.7
6.3 grams	4.41	3.49	20.9
Temperature	3.59	2.97	17.3
26.5-26.8°C.	2.92	2.41	17.5
	2.71	2.25	17.0
	2.60	2.18	16.2
	2.33	1.70	27.0
	2.33	1.71	26.6

TABLE 1 (Continued)

SPECIES	CC. OF O ₂ PER LITER		PERCENTAGE OF OXYGEN CONSUMED
	Inflow	Outflow	
	1.85	1.41	23.8
	1.85	1.41	23.8
	1.61	1.22	24.2
	1.61	1.22	24.2
	1.28	1.00	21.9
	1.28	1.00	21.9
<i>Podophthalmus vigil</i>	4.02	3.68	8.5
Weight	3.93	3.59	8.7
10.0 grams	3.16	2.73	13.6
Temperature	3.02	2.59	14.1
26.5-26.8°C.	2.95	2.56	13.2
	2.63	2.29	12.9
	2.48	2.16	12.9
	2.33	1.96	15.5
	2.13	1.87	12.2
	1.99	1.67	16.1
	1.79	1.53	14.5
	1.60	1.36	15.0
	1.41	1.19	15.6
	1.38	1.10	20.3
	1.34	0.98	26.9
Weight	4.53	4.19	7.5
11.1 grams	4.11	3.76	8.5
Temperature	3.78	3.41	9.8
26.3-26.6°C.	3.09	2.68	13.3
	3.00	2.64	12.0
	2.73	2.36	13.6
	2.38	2.08	12.6
	2.25	1.97	12.0
	2.01	1.74	13.4
	1.85	1.57	15.0
	1.75	1.50	14.3
	1.54	1.31	14.9
	1.43	1.40	16.1
	1.32	0.99	25.0
	1.20	0.97	19.1
	1.17	0.98	16.2

DISCUSSION AND CONCLUSIONS

With respect to adaptation in the consumption of oxygen, two main groups of animals can be distinguished: (1) those animals which show a *regulation* and (2) those showing an *adjustment*. The first group possesses mechanisms which permit the consumption of constant quantities of oxygen per unit of time, even when the oxygen tension varies markedly. They therefore actively regulate their respiration. The second group is unable to

do so. Consequently, their oxygen consumption varies (more or less) proportionately with the oxygen tension of the surroundings.

The Crustacea used in these experiments obviously belong to the large group of animals with an adjustable respiration. They lack the ability to regulate (at least to any appreciable extent) their oxygen consumption when the oxygen content of the water is altered. The oxygen consumption varies with the oxygen tension (Maloeuf, 1936) and according to Amberson *et al.* (1924) may even be directly proportional to it. Our experiments confirm this (Table 1). *Phymodius unguatus* and *Platypodia granulosa* seem to consume even less oxygen than expected when the oxygen content of the water is first reduced. After this initial period, however, oxygen consumption proportionate to the tension becomes apparent.

It has been claimed that many Crustacea do have a regulating mechanism in that they increase the rhythm of the beat of the scaphognathites and pleopods when the oxygen content of the water decreases (Munro Fox *et al.*, 1933, 1934; Johnson, 1936; Schlieper and Peters, 1937; van Heerdt and Krijgsman, 1939; van Heerdt, 1940). As these structures are the propellers by means of which the water flow is directed over the gills, an increase of the beat will bring the gills in contact with a larger quantity of water from which, consequently, more oxygen can be absorbed. In such cases some kind of regulation may be expected, not a typical adjustment as found in our experiments. Although, as mentioned before, we have been unable to make exact counts, in some cases an increase in the beat was noted when the oxygen tension of the water started to decrease. This would therefore point toward a regulation; but if so, then it must be very weak and is therefore not apparent in the direct results. However, when the utilization of oxygen (the oxygen consumed expressed as the percentage of the available oxygen in the water) is studied, such a weak regulation may eventually be found.

As long as the utilization remains constant when the oxygen tension of the water decreases, it means that there is little or no regulation, and the respiration is therefore of the adjustable type. When the utilization curve rises, it means that there is some regulation, that more oxygen is consumed than would be the case in the adjustment type of respiration. A drop of the curve means a decrease in oxygen consumption, as compared with the adjustment type of respiration.

Before the results with respect to the utilization of oxygen can be discussed, the question arises as to what can be the (primary) cause of regulation or adjustment in the process of respiration. Considering the simplest possibility, this is based on a limiting factor. Respiration being *de facto* an oxidation, the limiting factor can be either the oxidizable substances or the oxygen available. If there is an ample quantity of the former, the amount of oxygen reaching these substances must be regulated to maintain oxidation at a constant level. To increase (or decrease) this level, more (or less) oxygen must be admitted. Here oxygen is clearly the limiting factor. In the case of the oxidizable substances being the limiting factor, the rate of oxidation is determined by the amount of such substances made available by the organism.

An objection may be raised in that the possibility might exist that there is a complete tissue oxygen saturation in the organism which becomes unsaturated at lower tensions, resulting in increased utilization at that point. In that case, however, the utilization curve will steadily rise with decreasing oxygen tension of the water, because the quantity of oxygen consumed by the tissues remains constant. This is not the case (Figs. 1-7). Admittedly, the alternative between "fuel" (oxidizable substances) and available oxygen as limiting factors is probably too simple but is unavoidable at this time as far too little is known of the intracellular respiration processes in Crustacea to include them in the picture. As long as such processes in this

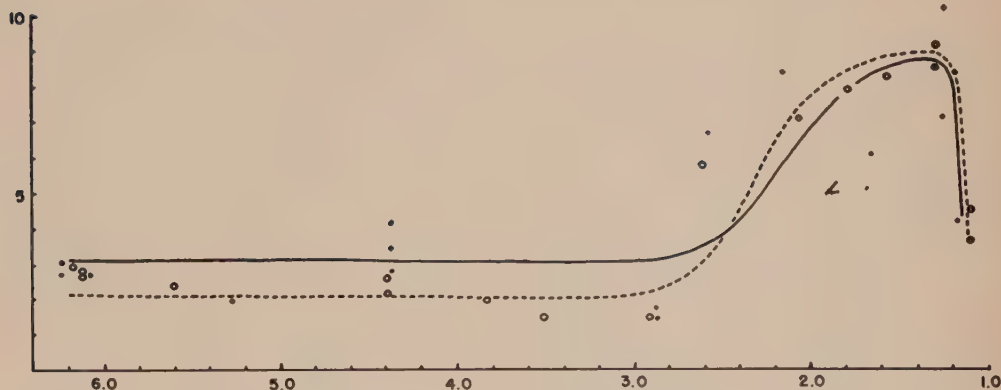


FIG. 1. Oxygen utilization in *Pseudozius caystrus*. Abscissa—cubic centimeters of oxygen per liter of water; ordinate—percentage of oxygen consumed from the oxygen available.

group of animals are not well understood, a simple picture seems preferable and justified.

According to our results (Table 1), the amount of oxygen consumed decreased with the decrease of the oxygen present over the entire range of the experiments. Oxygen seems, therefore, to be the limiting factor. If so, the utilization curve must run parallel to

the abscissa. But this is not the case for the entire curve. Figures 1–4 show, for example, that as soon as the oxygen content of the water reaches a certain low level (*Pseudozius* 2.8–3 cc. O_2/l , *Metopograpsus* 2.8–3.2 cc. O_2/l , *Calappa* 3.0–3.2 cc. O_2/l , and *Pseudosquilla* about 2.9 cc. O_2/l) the utilization curve rises. This points definitely toward a regulation,

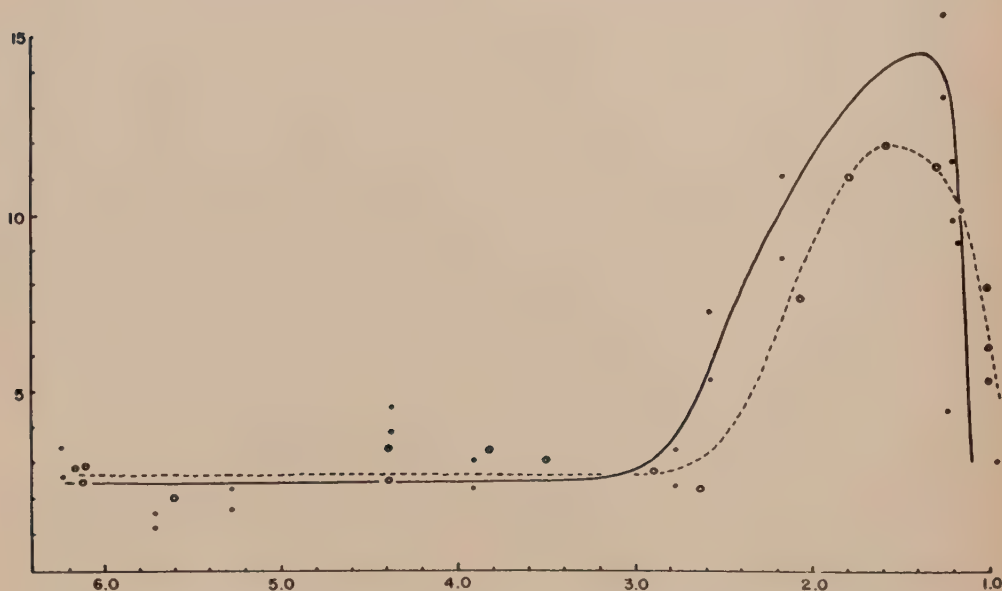


FIG. 2. Oxygen utilization in *Metopograpsus messor*. Abscissa—cubic centimeters of oxygen per liter of water; ordinate—percentage of oxygen consumed from the oxygen available.

which is probably not the result of a sudden increase of the rhythm of the beat of the scaphognathites or pleopods, because such a sudden increase was never observed. On the contrary, at low oxygen tensions these structures very often beat quite irregularly, but apparently more slowly. This means, therefore, that oxygen is no longer the limiting factor in oxygen consumption. The fact that the amount of available oxygen decreases whereas its utilization increases and the water propelling mechanisms do not show a sudden acceleration can have but one meaning: more oxidizable substances become available for (direct) oxidation. This must be the result

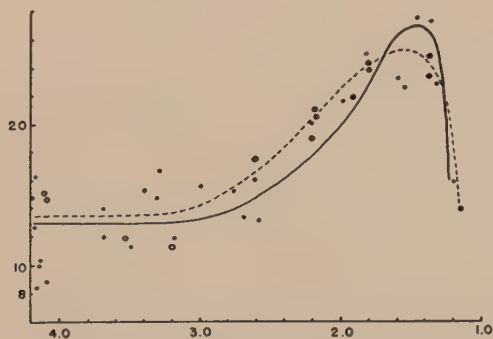


FIG. 3. Oxygen utilization in *Calappa hepatica*. Abscissa—cubic centimeters of oxygen per liter of water; ordinate—percentage of oxygen consumed from the oxygen available.

of a change in metabolic processes which produce such readily oxidizable substances. Such a metabolic mechanism must be considered an important "safety measure" to the animals, as they can now maintain life under conditions which would probably prove fatal without it. However, it does not actually change the animal from an "adjustment" into a "regulation" type, as the total oxygen consumption continues decreasing with the oxygen content of the water. A moment will come at which the amount of oxidizable substances set free in the tissues is no longer sufficient to maintain life with the available oxygen. Then the utilization curve will de-

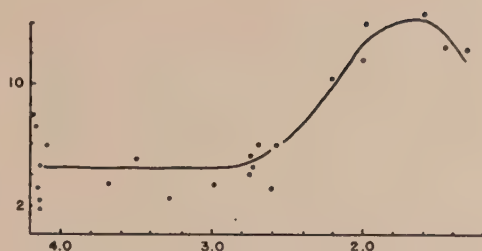


FIG. 4. Oxygen utilization in *Pseudosquilla ciliata*. Abscissa—cubic centimeters of oxygen per liter of water; ordinate—percentage of oxygen consumed from the oxygen available.

crease sharply (Figs. 1–7), and death will be the result in a comparatively short time. At the relatively high temperatures encountered in Hawaii, the crabs usually die in 1 to 2 hours when the water contains less than 0.96 cc. $O_2/l.$, but they stay alive for at least 3 hours when 1.4 cc. $O_2/l.$ is present. At lower temperatures, wherein the metabolism is at a much lower level, they seem to withstand lower oxygen tensions successfully. Jordan and Guittart (1938) reported, for instance, that at 13°C. *Potamobius fluviatilis* lived for 2.5 hours in water containing only 0.35 cc. $O_2/l.$, after which period the experiment was terminated.

The suggestion that certain substances used in respiration are liberated by the tissues, by

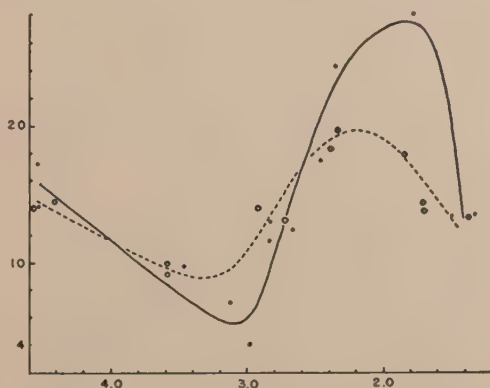


FIG. 5. Oxygen utilization in *Phymodius unguatus*. Abscissa—cubic centimeters of oxygen per liter of water; ordinate—percentage of oxygen consumed from the oxygen available.

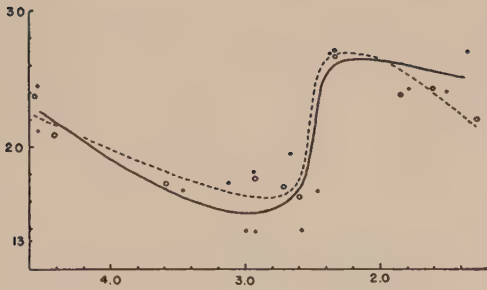


FIG. 6. Oxygen utilization in *Platypodia granulosa*. Abscissa—cubic centimeters of oxygen per liter of water; ordinate—percentage of oxygen consumed from the oxygen available.

some life process, at low oxygen tensions is not as hypothetical as it seems to be. Helff (1928) has already discussed the possibility of oxygen being secreted by the tissues, but this idea has been rejected, chiefly because of errors in his experimental method (Maloeuf, 1936). Recently Harnisch (1951), using a better technique, reached the same conclusion in his experiments on *Chironomus* larvae. He was able to prove this assumption correct by investigating the hemoglobin of the larvae spectrophotometrically: at very low oxygen tensions the hemoglobin contained more oxygen than would be possible without such a secretion. By observing the living animal continuously, he could actually observe the re-oxidation of the reduced hemoglobin. When, however, the oxygen reserve was consumed (probably because of a weakening of the life processes necessary to liberate the oxygen, which means that the latter was not present in reserve as free oxygen), re-oxidation of the hemoglobin ceased. Koenen (1951) also mentioned the sudden rise of oxygen consumption at low oxygen tensions in her experiments.

The utilization curves of *Phymodius* and *Platypodia* (Figs. 5, 6) slope down in the beginning of the experiment. This may be caused by an ineffective propelling mechanism. At 3–3.2 cc. O_2/l . (*Phymodius*) and 2.9–3.1 cc. O_2/l . (*Platypodia*), we again get the sudden

rise of the curve, followed by the now familiar decrease at 1.8–2.2 cc. O_2/l .

The mud-dweller *Podophthalmus*, on the other hand, shows from the beginning a slight increase of the utilization curve (Fig. 7) which may be due to a more effective stroke of the scaphognathites. Some regulation might be expected in an animal living in a habitat that is usually poor in oxygen. Because of the adaptation to such a habitat, we would also expect the safety measure to occur at a lower oxygen tension than in animals normally living in much better aerated water. The curve shows, indeed, a steep rise at 1.5 cc. O_2/l . The final drop seems to occur at around 1.3 cc. O_2/l . How do these data fit into the ecological pattern? We cannot expect the safety measure to be thrown into gear at very low oxygen tensions in *Metopograpsus* (practically an air-breather), *Pseudozoeus* (which lives in well-aerated water of the tidal zone), or *Phymodius* and *Platypodia* (which live on corals). Here, due to currents and, during the day, to photosynthesis by algae, the water is certainly not poor in oxygen. *Calappa* and *Pseudosquilla*, living on sandy flats in shallow water, seem to be in a less favorable situation. However, the organic matter present is not very abundant (as compared with organic mud), and minute algae covering the surface will produce during the day a fairly abundant

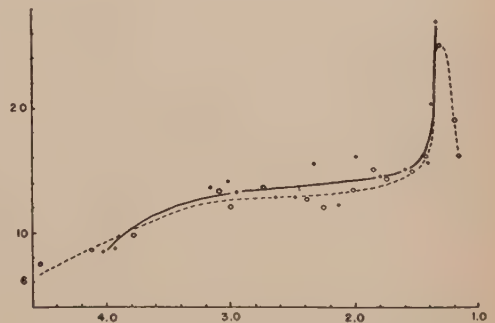


FIG. 7. Oxygen utilization in *Podophthalmus vigil*. Abscissa—cubic centimeters of oxygen per liter of water; ordinate—percentage of oxygen consumed from the oxygen available.

supply of oxygen, so that only during the night an appreciable drop of the oxygen tension of the water may be expected. Again, currents and tides will counteract this drop in part, so that the local oxygen deficiency is probably not very great.

With *Podophthalmus* the picture is a different one. The crab, which swims surprisingly little and remains buried in the mud during the day, lives in a habitat decidedly poor in oxygen. A physiological adaptation could be expected and is apparent: utilization shows a gradual but definite increase until a level of 3 cc. O₂/l. is reached, after which it increases more slowly and evenly until the water contains 1.4 cc. O₂/l., at which point the safety measure is thrown into gear.

SUMMARY

1. The oxygen consumption of *Metopograpsus messor* Forsk¹, *Pseudozius castrus* Adam and White, *Phymodius unguatus* Milne Edwards, *Platypodia granulosa* Rüppell, *Calappa hepatica* Linn., *Pseudosquilla ciliata* Miers, and *Podophthalmus vigil* Fabricius in running sea water of varying oxygen tensions was studied. All these animals belong to the so-called adjustable type of respirers, in that oxygen consumption decreases more or less proportionately with the oxygen tension of the water.

2. Analysis of the utilization of oxygen (percentage of oxygen consumed from the available oxygen) shows that at low oxygen tensions the metabolism of the animals changes, a change which counteracts partly the lack of oxygen of the surroundings.

3. The ecological importance of the different types of oxygen utilization is discussed.

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A Simple Apparatus for Truing Paraffin Blocks¹

by

Donald C. Matthews²

• Truing paraffin blocks occasionally proposes an arduous task for the introductory microtechnique student. When he is acquiring proficiency in staining techniques curved ribbons admittedly serve his needs as well as straight ones. Moreover, if the curvature of the ribbon becomes too severe he can remove the block, trim it, and the subsequent loss of sections is, at this stage in his training, of no serious consequence. However, a certain laxity regarding the importance of truing the paraffin block develops when this technique is permitted. Observations indicate that although

the student may learn to square the surface of his paraffin block, he rarely succeeds in trimming the vertical sides parallel. Therefore, when he is requested to mount the complete serial sections of, say, a small embryo on four or five slides many specimens are ruined before this apparently stringent requirement is satisfied.

To conserve both time and materials paraffin blocks are now trued in our laboratory by a simple, inexpensive apparatus. As illustrated in the figure it consists of three parts 1) a small vise, the curved jaws of which are planed to provide a smooth, flat surface; 2) mounting blocks, the heads of which are square; and 3) a U-shaped wrench, the upper surface of which is provided with two vertical cutting guides.

The wrench is cut from brass stock $\frac{1}{8}$ inch thick and 2 inches wide. The throat is planed to provide an opening exactly 1 inch wide and $1\frac{1}{4}$ inches deep. Holes $\frac{1}{8}$

1. Contribution No. 50, Hawaii Marine Laboratory.

2. Department of Zoology and Entomology, University of Hawaii, Manuscript received December 28, 1953.

inch in diameter are drilled $\frac{1}{4}$ inch from the sides and from the open end of the wrench, tapped, and the threaded, 1 inch long vertical cutting guides are inserted. A small chain is attached to the handle of the wrench to secure it to the vise.

The customary circular mounting blocks are converted by sweating on now, perfectly square mounting heads. These are ground to fit snugly into the throat of the wrench.

In operation the paraffin block is mounted in the usual way and the shank (or ball) of the mounting block is secured in the vise. The under surface of the mounting block should rest flush with the smooth, flat surface of the vise. The wrench is placed on the flat surface of the vise and moved horizontally to engage the square mounting block. When the paraffin block extends past the vertical cutting guides, a single-edge razor blade, held against the guides, is used to make the vertical cut. The $\frac{1}{8}$ inch thickness of the wrench prevents the cut from extending into the supporting paraffin base. Depending upon the desired size of the finished paraffin block, the wrench can either be moved still farther horizontally and the opposite side cut parallel or removed and

the square mounting block engaged from the opposite direction. Usually opposite parallel sides are cut by a single engagement of the wrench. The wrench is then removed and the square head of the mounting block engaged at right angles to the first cut. Thus, by changing the wrench only once, it is possible to cut all four sides vertical and parallel. No further trimming is necessary if 1) the mounting heads are true and if these are secured flush with the smooth flat surface of the vise, 2) the wrench is true and fits the square mounting heads tightly, and 3) the upright guide posts are truly vertical and placed equidistant from the base.

Obviously, neither this nor other truing machines (*vide* Gatenby and Beams, 1950: 83) guarantee true cross sections; such are possible only when the object to be sectioned is straight and properly oriented to the longitudinal axis of the block. These conditions satisfied, however, this apparatus, even in inexperienced hands, assures not only straight ribbons but true cross-sections.

reference

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RECORDS OF HAWAIIAN CTENOPHORA¹

DONALD C. MATTHEWS

Department of Zoology and Entomology, University of Hawaii

Although published accounts of Ctenophora indicate their paucity in Hawaiian waters, actually representatives of all orders are now known to occur (Cydippida, Lobata, Cestida, Beroida, Platyctenea). This paper reviews the earlier described Hawaiian ctenophores and records species not previously reported.

CYDIPPIDA

Hormiphora palmata was reported among the few Ctenophora collected by the "Albatross" in Hawaiian waters (Mayer, 1906; Bigelow, 1912), but no further accounts of cydippids have appeared. The ctenophores mentioned by Edmondson (1946) as occurring in the shallow waters of Waikiki reef, Oahu, and in the surface waters of Pearl Harbor, Oahu, were undetermined, but are obviously cydippids. Both his description and figure of the swimming plates and pinnate tentacles of these small, spherical ctenophores serve to assign them to this order. These and undetermined cydippids commonly taken in Kaneohe Bay, Oahu, attest their prevalence in Hawaiian waters.

LOBATA

No published accounts of Hawaiian lobatids have been found. It should be recorded, however, that Drs. Albert Banner and Robert Hiatt of the Zoology Department, University of Hawaii, collected a small, colorless representative of this order at Hanauma Bay, Oahu, in March, 1951. This specimen was seriously damaged when preserved but its two large oral lobes and unsheathed tentacles unmistakably place it in this order.

CESTIDA

No published records of Hawaiian cestids are known to the writer. While skin diving at Hanauma Bay, Oahu, in March, 1951, Drs. Banner and Hiatt saw several small, ribbon-like cestids which they were unable to collect. Circumstances under which these transparent forms were observed made it impossible to determine the nature of their four subtentacular canals (a character used to distinguish *Velamen* from *Cestum*). If these specimens were mature, their small size, approximately 15 cm. long (actually the morphological width), suggests the genus *Velamen* (Hyman, 1940).

¹Contribution No. 51, Hawaiian Marine Laboratory.

BEROIDA

The only published account of Hawaiian beroids is that of Bigelow (*op.cit.*). The only Hawaiian species (*Beroë forskalii*) was found at 300 fathoms. It appears rather unlikely that members of this order frequent shallow reef waters.

PLATYCTENEA

A search for platycteneids was begun in 1951. The probability of collecting certain genera was remote. The orders of Alcyonaria (Alcyonaceae, Gorgonaceae, Pennatulaceae), which have representatives of the genus *Coeloplana* (*C. agniae*, *C. sophiae*, *C. dubosquii*, etc.) (Dawydoff, 1938) in Indo-Chinese waters, are not found in the shallow waters of Hawaiian reefs. *Tjalfiella tristoma* (Mortensen, 1910) attached to *Umbellula* found on the west coast of Greenland would in all probability be absent from the warm waters of Hawaii. It also appeared very unlikely, with one possible exception, that the Japanese species *Coeloplana willeyi*, *C. mitsukurii* (Abbott, 1902) *Coeloplana bocki*, *Lyrocteis imperatoris* (Komai, 1920, 1942) would occur here since the general trend of the shore fauna of the central Pacific area has been from the Indian Ocean (Edmondson, *op.cit.*).

Two known possibilities remained. Within the pelagic tunicate, *Salpa fusiformis*, taken in the vicinity of Misake (Japan), Komai (1922) observed the bizarre platyctenid, *Gastrodes parasiticum*. As this salp is common in Hawaiian plankton hauls, it seemed reasonable to expect *Gastrodes*. J. L. Yount has examined thousands of salps including *Salpa fusiformis* in the plankton hauls of the Pacific Oceanic Fishery Investigations (U. S. Fish and Wildlife) but has not observed any *Gastrodes parasiticum* to date.

A more promising possibility of finding a platyctenid was offered by the slate-pencil urchin (*Heterocentrotus mamillatus*). Dawydoff (1938) collected *Coeloplana weilli* on this urchin, in the region of Réam (Gulf of Siam, Cambodia). This same species of urchin has been obtained on the reef at the Hawaii Marine Laboratory. Hundreds of these have been examined but no coeloplanids have been found so far.

Quite by chance a minute platyctenid was observed creeping over an alga (*Hypnea nidifica*) collected on the reef at the Hawaii Marine Laboratory, December 31, 1952. An additional solitary specimen of approximately the same developmental stage has since been collected on this alga.

This pale, slightly yellowish-green specimen when fully extended measured 3-5 mm along its tentacular axis. The slightest jar of the dissecting microscope caused it to contract rapidly, assuming an almost spherical form slightly less than 3 mm in diameter. In this contracted state it was less hyaline than when relaxed. The body appeared uniformly pigmented except for a slightly heavier pigmentation at the bases of the tentacular sheaths and along the main tentacular axis. Under higher magnification extremely minute, bright red spots were seen which formed a narrow, irregular band on the peripheral, aboral surface.

The tentacles were more often alternately extended although occasionally they "flowed" simultaneously from their tentacular sheaths. In their usual position they measured 2-3 times the length of the body taken along the tentacular axis. They were typically cydippid-like and

each pinnate branch moved quite independently of the others. The tentacles were extended slowly, but were retracted quickly.

The sense-organ was clearly discernible as a small rounded area in the center of the aboral surface when the animal was relaxed. Komai (1922) described an apparent small rounded area which in reality was a deep depression along the tentacular axis. In its center was a spherical otolithic mass. Two elevated semicircular polar plates occupied a sagittal position on either side of the depression, but their peripheries were unlobed and they were devoid of cilia.

Just outside the border of each polar plate a prominent excretory pore was located. These pores, together with the aboral sense organ, appeared and disappeared as the gastrovascular system relaxed and contracted. This constant rise and fall produced an illusion of opening closing of the pores, however, nothing was actually extruded.

Eight small, teat-like papillae, one at the end of each gastrovascular canal, were arranged along the tentacular axis roughly in two "longitudinal" rows of four. These were so hyaline that small particles carried by gastrovascular currents were seen gyrating within them.

Since comb-rows were absent, this platyctenid undoubtedly belongs to the genus *Coeloplana*. The size, color, number of dorsal papillae and the nature of the polar plates do not conform with those of any known species. Its small size, the presence of only eight aboral papillae, the absence of cilia on the unlobed polar plates, and the absence of gonads strongly suggest immaturity. Until additional specimens are found, this platyctenid is assigned temporarily to *Coeloplana dubosequii* (Dawydoff, *op.cit.*).

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A Comparative Study of the Spermatophores of three Scyllarid Lobsters (*Parribacus antarcticus*, *Scyllarides squammosus*, and *Scyllarus martensii*)

By DONALD C. MATTHEWS

(From the Department of Zoology and Entomology, University of Hawaii)

SUMMARY

1. In *Parribacus antarcticus* and *Scyllarus martensii* mitotic division of germinal epithelial cells produces primary spermatocytes, whereas in *Scyllarides squammosus* this function of the germinal epithelium is limited to comparatively few large, oocyte-like cells.

2. Metamorphosing spermatids in all three species are expelled from the sacculi of the testis by the rhythmical activity of their germinal epithelium. This probably accounts also for the clumping of the spermatozoa in the collecting tubule; each clump represents the extended contents of a single sacculus.

3. In *Scyllarus martensii* and *Scyllarides squammosus* a continuous, cord-like, encapsulated spermatogenic mass traverses the vasa deferentia, whereas in *Parribacus antarcticus* the spermatogenic mass separates into distinct ampullae which become encapsulated and are further provided with an enveloping sheath. This sheath between adjacent ampullae becomes ribbon-like, twists, and ultimately forms short, doubly twisted peduncles.

4. A secretion of the typhlosole in all three species surrounds the completed spermatophores and forms the homogeneous matrix.

5. Although these three species are anatomically similar, the spermatophores of *Scyllarus martensii* and *Scyllarides squammosus* resemble non-pedunculate spermatophores of the palinurids, the astacids, the homarids, and the nephropsids, whereas those of *Parribacus antarcticus* more nearly resemble the pedunculate spermatophores of certain pagurids.

6. Spermatophoric evidence above does not justify the inference that *Parribacus antarcticus* occupies a systematic position intermediate between the *Macrura* and the *Anomura*.

INTRODUCTION

ALTHOUGH the origin and nature of certain rock lobster spermatophores have been investigated (Andrews, 1912; Matthews, 1954a), comparative studies have been neglected. The year-round availability in Hawaii of species embracing three scyllarid genera (*Parribacus*, *Scyllarides*, *Scyllarus*) is propitious for such a study. Such a comparison should both extend our knowledge of scyllarid biology and afford a clearer insight into the nature of their spermatophores.

Although Andrews's description (1912, p. 183) of the external spermatophoric mass of *Parribacus antarcticus* is correct, his reference to an 'internal . . . matrix enclosing tubular cavities' is erroneous (Matthews, 1954a). Calman's general statement (1909, p. 290) about the spermatophores of the *Macrura* is correct, but his specific reference to the spermatophores of *Scyllarus* [sp.?],

as will be shown subsequently, is incorrect. Since our knowledge of scyllarid spermatophores is based largely on these conflicting accounts, need for clarification is apparent.

METHODS AND TECHNIQUES

Both male and female *Parribacus antarcticus* (Lund), *Scyllarides squammosus* (Milne Edwards), and *Scyllarus martensii* (Pfeffer) obtained from fishermen and from the Honolulu Aquarium during the year 1953 were used in this study.



FIG. 1. Composite drawing of the male reproductive system as revealed by dissection of *Parribacus antarcticus*, *Scyllarides squammosus*, and *Scyllarus martensii*. *a*, anterior portions of testes; *b*, pyloric region of stomach; *c*, transverse bridge; *d*, intestine; *e*, mid-portions of testes; *f*, posterior portions of testes; *g*, proximal portion of vas deferens; *h*, hyaline line; *i*, enlarged distal portion of vas deferens.

All dissections were made on living, non-anaesthetized specimens immersed in sea water. The carapace was opened quickly and the internal organs overlying the reproductive system were removed.

Right vasa deferentia of each species were either fixed in Bouin's fluid, washed in alcohol (70 per cent.), cleared in dioxane, embedded in Tissuemat (54–56° C.), sectioned at 10 μ , and stained in standard alum haematoxylin and eosin; or they were fixed in Champy's fluid, washed in running water

(24 hours), dehydrated in alcohol, cleared in cedarwood oil, infiltrated with xylene, embedded in Tissuemat (54–56° C.), sectioned at 4–6 μ , and stained in iron haematoxylin. This latter method was also used for those ovaries and testes which were sectioned.

Left vasa deferentia of each species were immersed for 10–30 minutes in an aqueous solution of toluidin blue (1:10,000), teased open in sea water, and their vitally stained contents studied and drawn.

OBSERVATIONS

The morphology of the testes and the vasa deferentia

The mature testes of these three species are macroscopically similar. Freed of overlying tissues all resemble an elongate H, the right and left sides being joined by a transverse bridge (fig. 1, *c*) immediately posterior to the junction of the pyloric region of the stomach (*b*) and the intestine (*d*). Occasionally the anterior portions of the testes (*a*) bifurcate, although the posterior portion (*f*), which lies contiguous with the digestive tract (*d*), is unaltered. The testis is composed of a highly coiled, continuous, thin-walled tube into which innumerable sacculi (fig. 6, *a*) open.

The mature vasa deferentia emerge from the mid-portions (*e*) of the testis. They are macroscopically dissimilar in the three species. Moreover, the right and left proximal portion (*g*) of the vas deferens of a single specimen may vary as much as those of different species. In all species the enlarged distal portion (*i*) which opens on the coxopodite of the fifth pereopod is less varied. This portion in all three species is marked by a distinct hyaline line (*h*).

Even when the vasa deferentia are quickly exposed in dissection, they fail to exhibit muscular contraction. This fact, together with their opacity, prevents one from observing the mechanics of the development of the spermatophores. However, by sectioning and vital staining, the otherwise obscure effects of contractions of the unaltered vasa deferentia are discernible.

Histology of the testes and the vasa deferentia

Sections through immature sacculi of *Parribacus antarcticus* (fig. 2, A) closely resemble those of *Scyllarus martensii* (fig. 2, B). In both species, sacculi in all stages of development are observed. Although there are small differences in saccular size, these vary as much within a species as between those of different species. From observations of hundreds of sacculi in both *Parribacus antarcticus* and *Scyllarus martensii* the author is of the opinion that those of *Parribacus antarcticus* are slightly larger. The connective tissue (*a*) which envelops the sacculi in both species is approximately of equal thickness (3 μ). The similarity of sacculi is further attested by the general likeness of the germinal epithelium (*b*) and the primary spermatocytes (*c*). In both species these cells are of approximately the same size (20 μ). In addition the immature sacculi of both species exhibit sustentacular-like cells (*d*) with indistinct cytoplasm and strongly chromophil nuclei, but their origin and method of

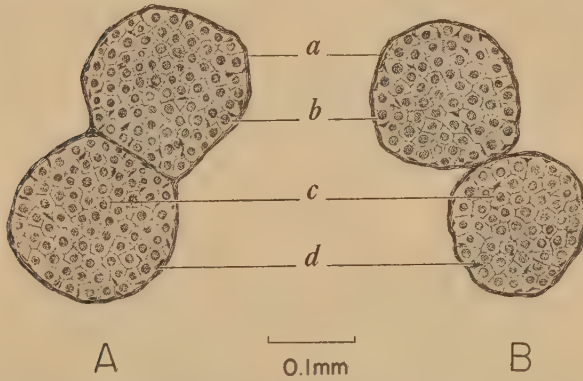


FIG. 2. Camera lucida drawing of sections through immature sacculi of A, *Parribacus antarcticus*, and B, *Scyllarus martensii*, showing: a, connective tissue; b, germinal epithelium; c, primary spermatocytes; d, sustentacular-like cells.

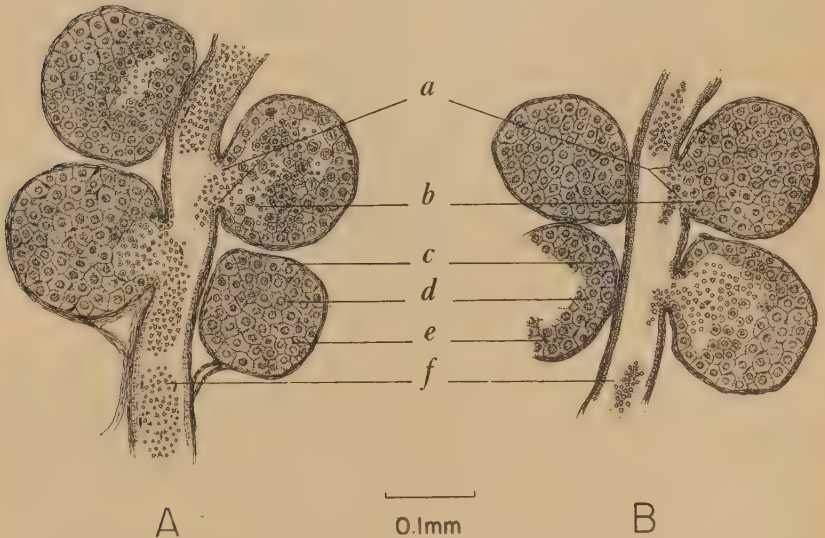


FIG. 3. Camera lucida drawing of sections through mature sacculi of A, *Parribacus antarcticus*, and B, *Scyllarus martensii*, showing: a, openings into collecting tubules; b, spermatids; c, germinal epithelial cells; d, primary spermatocytes; e, sustentacular-like cells; f, clumping of metamorphosing spermatids.

multiplication is obscure. When first observed, these cells lie contiguous with the germinal epithelium, an association which suggests but does not prove their origin. Concurrent with their increase in number, the meiotic divisions of the spermatocytes produce large numbers of spermatids.

Although many mature sacculi are seen, few reveal their actual opening into the collecting tubule (fig. 3, *a*); yet upon these sections in both *Parribacus antarcticus* (fig. 3, *A*) and *Scyllarus martensii* (fig. 3, *B*) depends our understanding of saccular activity. Concurrently with the metamorphosing of the

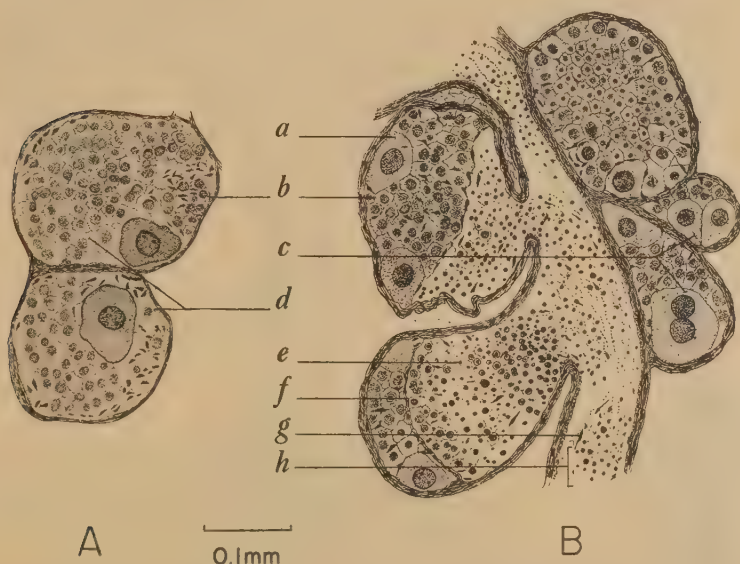


FIG. 4. Camera lucida drawing of sections of A, immature sacculi, and B, mature sacculi of *Scyllarides squammosus*, showing: *a*, oocyte-like cell; *b*, germinal epithelial cells; *c*, oocyte-like cells dividing; *d*, primary spermatocytes; *e*, spermatids; *f*, delimiting wall of sustentacular-like cells; *g*, sustentacular-like cells in tubule; *h*, clumping of metamorphosing spermatids in tubule.

spermatids (*b*), the germinal epithelial cells (*c*) renew their mitotic activity and again produce primary spermatocytes (*d*), which, as they fill the sacculi, expel the metamorphosing spermatids. This rhythmical activity of the germinal epithelium probably accounts also for the clumping of the metamorphosing spermatids in the tubule, each clump (*f*) representing the extruded contents of a single sacculus. It was not determined whether the sustentacular-like cells (*e*), some of which accompany the metamorphosing spermatids into the tubule, aid in the clumping process or simply serve as nutritive cells.

Although the sacculi of *Scyllarides squammosus* (fig. 4) are in general like those of *Parribacus antarcticus* and *Scyllarus martensii*, dissimilarity is at once apparent by the anomalous appearance of bizarre, oocyte-like cells (*a*). Their presence suggests an ovitesticis possibly resulting from certain castration-parasites (*Altheles*, *Chlorogaster*, *Peltogaster*, &c.); however, examination

reveals neither evidence of castration-parasites nor secondary sexual characters. These inquiline, oocyte-like cells are further misleading because in osmium tetroxide preparations they exhibit lipid cytoplasmic inclusions comparable to those of normal oocytes. This evidence simply attests their general oocyte-like appearance, but further study discloses their true spermatogenetic function.

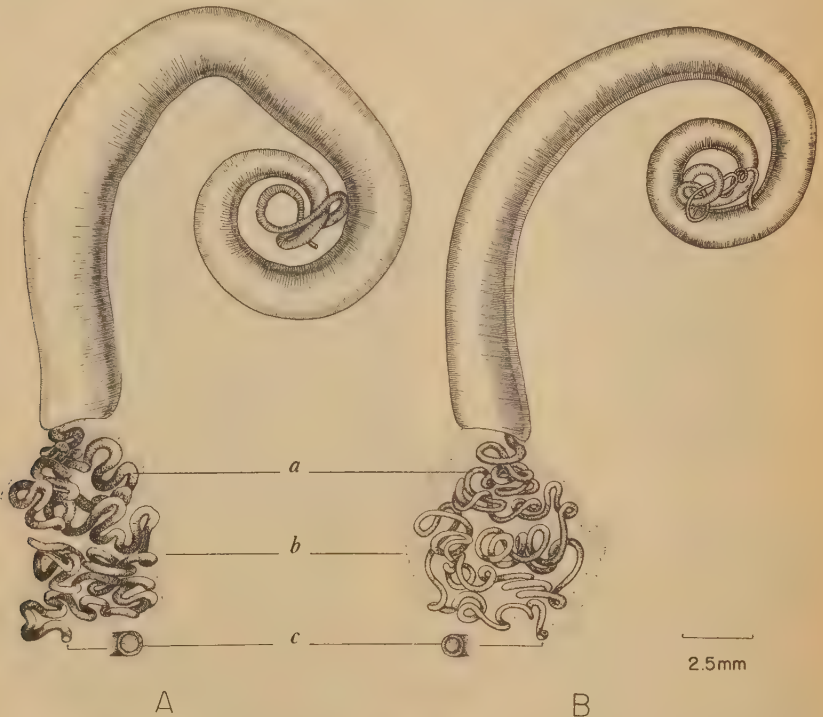


FIG. 5. Extruded masses from vitally stained portions of the enlarged vasa deferentia of A, *Scyllarides squammosus*, and B, *Scyllarus martensii* showing: a, continuous, thread-like spermatophore; b, homogeneous matrix; c, capsule (enlarged).

Apparently in this species each germinal epithelial cell (b) possesses the potentiality for the production of primary spermatocytes, but actually this function is restricted to comparatively few cells. While other germinal epithelial cells remain unaltered, these few increase greatly in size (up to $135\ \mu$), divide (c) and redivide mitotically, subsequently filling the sacculus with primary spermatocytes (d). These, as in the two species previously described, undergo meiotic divisions, filling the sacculi with spermatids (e).

In this species also, then, the rhythmical expulsion of the metamorphosing spermatids is evidenced as new primary spermatocytes are formed. Whereas in *Parribacus antarcticus* and *Scyllarus martensii* the new crop of primary

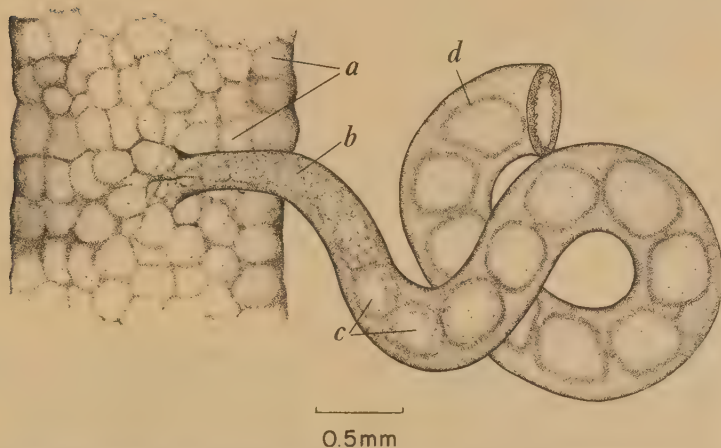


FIG. 6. Vitally stained portion of the testis and proximal vas deferens of *Parribacus antarcticus*, showing: *a*, sacculi of testis; *b*, undifferentiated spermatogenic mass; *c*, moniliform portion of spermatogenic mass; *d*, distinct ampulla of sperm with thick-walled capsule.

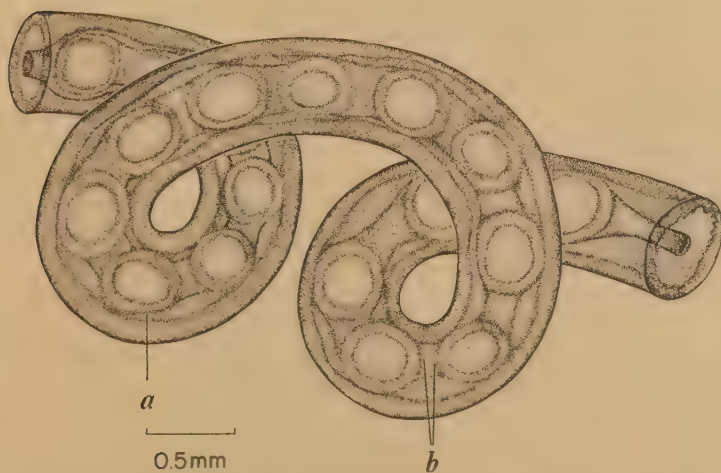


FIG. 7. Vitally stained portion of the proximal vas deferens of *Parribacus antarcticus* (slightly posterior to fig. 6), showing: *a*, sheath-forming material enveloping the already encapsulated ampulla; *b*, sheath-forming material filling spaces between adjacent ampullae.

spermatocytes is not sharply marked off from the metamorphosing spermatids, in *Scyllarides squammosus* they are delimited by a thin wall of sustentacular-like cells (*f*). As in the two species previously described, the fate of the sustentacular cells (*g*) which accompany the metamorphosing spermatids into the collecting tubule is obscure.

Vital staining of the vasa deferentia

Vital staining of the vasa deferentia reveals in *Scyllarides squammosus* (fig. 5, A) and *Scyllarus martensii* (fig. 5, B) a continuous, thread-like spermatophore (*a*). In these two species the spermatophoric mass, probably by muscular contractions of the vasa deferentia, is both moved along and moulded in conformity to their lumina, which are circular in transverse section. Moreover,

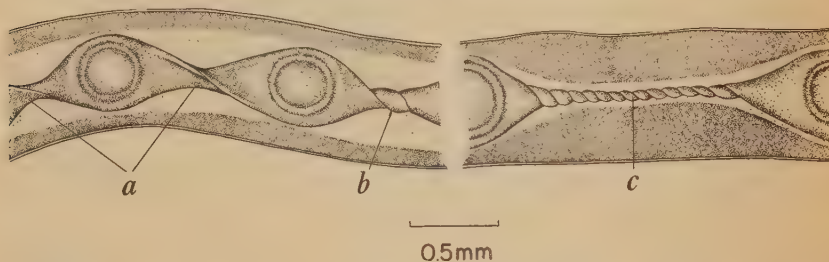


FIG. 8. Vitrally stained portions of the proximal vas deferens of *Parribacus antarcticus* (slightly posterior to fig. 7), showing: *a*, ribbon-like sheath between adjacent ampullae; *b*, *c*, chalaza-like twisting of sheath.

as the walls of the vasa deferentia thicken, a secretion from crypt-like folds of the epithelium surrounds the cord-like mass and forms the capsule (*c*). In these two species, as the lumina of the vasa deferentia enlarge, the encapsulated, cord-like masses become highly coiled and folded; however, they remain continuous throughout. As they traverse the enlarged portion of the vasa deferentia these masses are enveloped by a secretion of the typhlosole. This secretion forms the homogeneous matrix (*b*).

Since vital staining of the vas deferens of *Parribacus antarcticus* has been discussed in a previous paper (Matthews, 1954*a*), only those points pertinent to this comparative study will now be summarized. By vital staining (fig. 6) the undifferentiated spermatogenic mass (*b*) is seen emerging from the sacculi of the testis (*a*). This mass, probably by contractions of the walls of the proximal portion of the vas deferens, is moved along, made moniliform (*c*), and finally broken into distinct ampullae. A secretion from the crypt-like folds of the epithelium surrounds each ampulla and forms a thick-walled capsule (*d*). A new secretion from the epithelial cells lining the vas deferens (fig. 7) envelops the already encapsulated ampullae (*a*) and fills the spaces between them (*b*). This secretion forms the sheath. This sheath (fig. 8) between adjacent ampullae becomes ribbon-like (*a*), probably as a result of muscular contraction of the walls of the vas deferens; and as the ampullae traverse the

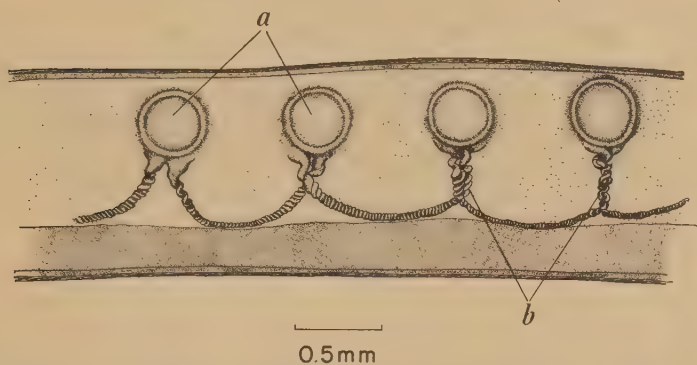


FIG. 9. Vitally stained portion of the distal vas deferens of *Parribacus antarcticus*, showing: *a*, raised ampullae; *b*, short, doubly twisted peduncles.

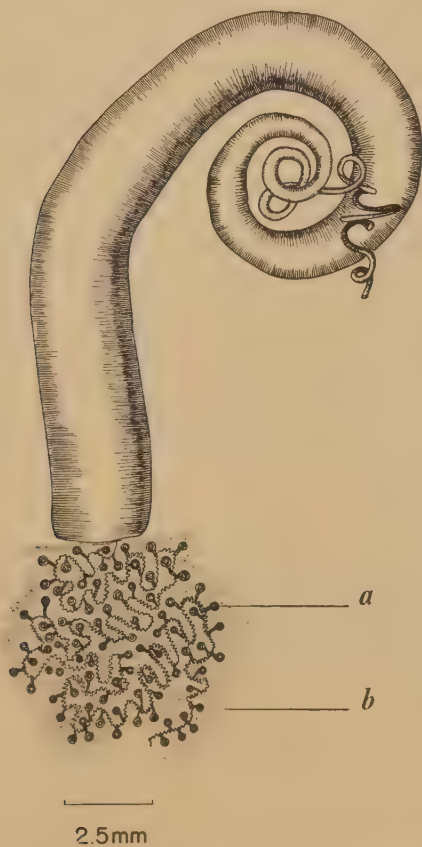


FIG. 10. Extruded mass from vitally stained portion of the enlarged vas deferens of *Parribacus antarcticus*, showing: *a*, ampulla of spermatozoa raised on short peduncles; *b*, homogeneous matrix.

coiled vas deferens, this ribbon-like sheath becomes twisted (*b, c*) so as to resemble chalazae. Continued twisting (fig. 9) causes these to entwine, raising the ampullae (*a*) on short doubly twisted peduncles (*b*). As in the two previously described species, a secretion from the typhlosole of the enlarged distal portion of the vas deferens (fig. 10) now envelops the completed spermatophore (*a*) and forms the homogeneous matrix (*b*). Whereas *Scyllarides squammosus* is set apart by its saccular activities, *Parribacus antarcticus* is set apart by the activity of its vasa deferentia.

DISCUSSION

All recorded observations indicate that the palinurids (with the possible exception of *Yasus lalandii*, von Bonde, 1936), the astacids, the homarids, and the nephropsids produce continuous, highly convoluted spermatophores embedded in homogeneous matrices (*Panulirus interruptus* (Allen, 1916; Fasten, 1917; Wilson, 1948); *P. argus* (Crawford and De Smidt, 1923); *P. penicillatus* (Matthews, 1951); *Potamobius trowbridgii* (Andrews, 1931); *Homarus americanus* (Herrick, 1895); and *Enoplometopus occidentalis* (Matthews, 1954b)). These recorded observations are in accord with Calman's (1909) general statement that 'in most Macrura the spermatozoa are enclosed in a sheath, forming a continuous cord-like mass'. Moreover, he states that 'in the Anomura this is broken up into separate spermatophores attached by one end in a row on a strip of membrane'. The Macrura therefore produce non-pedunculate spermatophores whereas the Anomura produce pedunculate spermatophores (see Mouchet, 1930, 1931; Matthews, 1953).

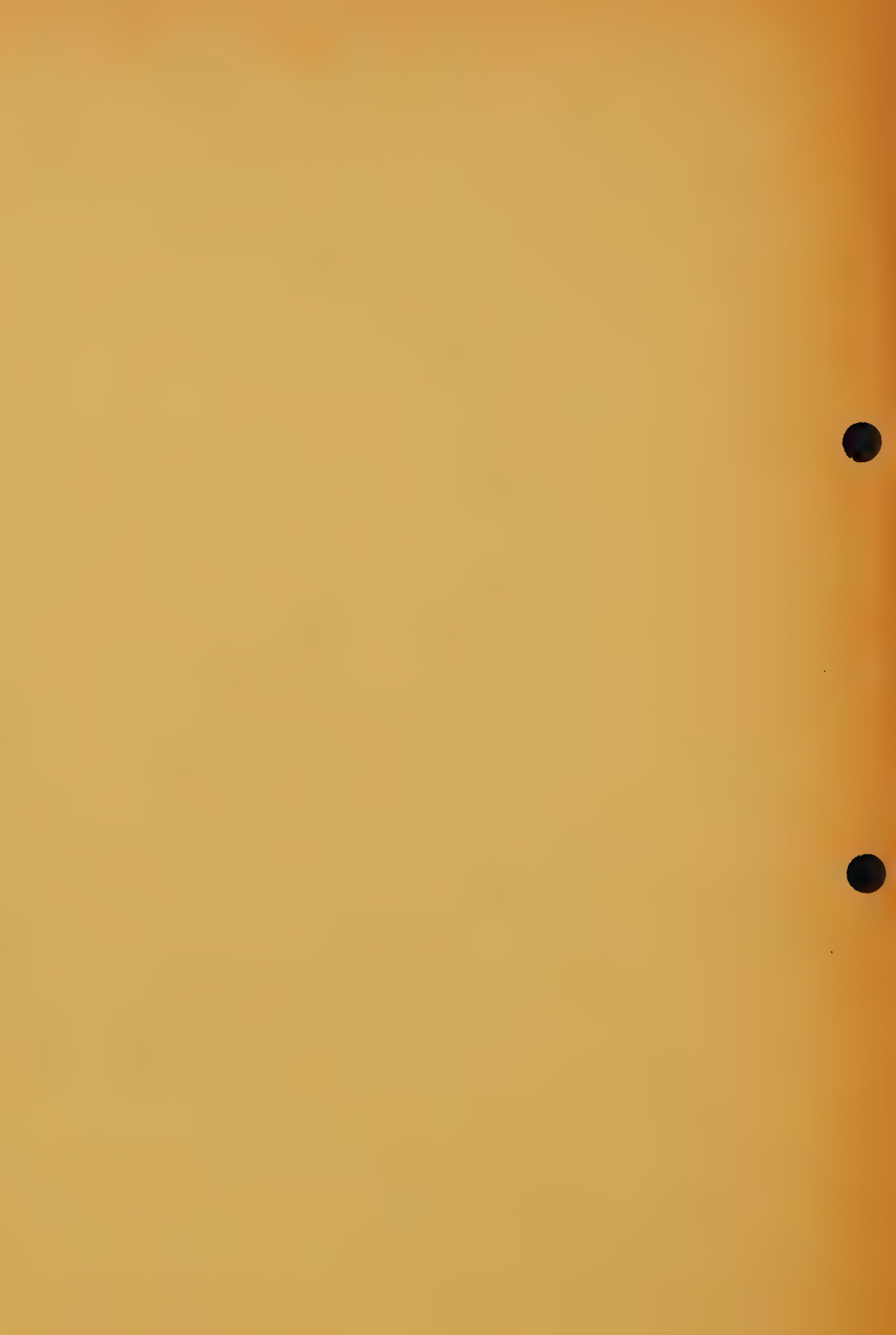
The spermatophores of *Scyllarides squammosus* and *Scyllarus martensii* clearly belong to the non-pedunculate Macrura, whereas those of *Parribacus antarcticus* appear intermediate between the non-pedunculate Macrura and the pedunculate Anomura. However, this is insufficient evidence that *Parribacus antarcticus* is intermediate between these two groups. Anatomical, embryological, and serological evidence should accompany such evidence from the spermatophores, and this should be obtained from many species, representing many genera.

The results of this study justify two conclusions: (1) species of otherwise closely related genera do not necessarily produce similar spermatophores, and (2) the origin of peduncles may have been only the fortuitous occurrence of mechanical and physiological activities of the vas deferens, inasmuch as those of *Parribacus antarcticus* fail to elevate the ampullae for the subsequent dispersal of the spermatozoa.

This paper forms Contribution No. 52 of the Hawaii Marine Laboratory.

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The Taxonomy of the Salpidae (Tunicata) of the
Central Pacific Ocean

JAMES L. YOUNT

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The Taxonomy of the Salpidae (Tunicata) of the Central Pacific Ocean¹

JAMES L. YOUNT

INTRODUCTION

KNOWLEDGE OF THE SALPS of the central Pacific Ocean is scanty as heretofore they have been studied only in conjunction with extensive collections, such as those of the "Challenger" and "Albatross" (Herdman, 1888; Metcalf, 1918), from large areas. The present paper, which is limited to a discussion of taxonomy and morphology, is based on large collections that have recently become available. A further report on distribution and ecology is in preparation.

Although much of the present paper is of necessity similar to previously published work, especially those portions describing muscle arrangement, the descriptions are based on original study unless otherwise stated. A new method of study for salps, also applicable to many other planktonic animals, was used and is here described.

Species of the genus *Salpa* were arranged into a number of related subgenera by Metcalf (1918) as follows: *Cyclosalpa*, *Brooksia*, *Apsteinia*, *Salpa*, *Ritteria*, *Thetys*, *Pegea*, *Traustedtia*, *Thalia*, and *Iasis*. Some of these names originated with earlier investigators. Because

of prior usage, it was necessary to replace *Ritteria* by *Ritteriella*, and *Apsteinia* by *Ihleia*, which he did in 1919. All these subgenera were raised to the rank of genera by Ihle and Ihle-Landenberg (1933), who at the same time added the genus *Metcalfina* for *Salpa hexagona* Quoy and Gaimard, 1824. This classification is in general use today and is followed here, with the addition of the genera *Helicosalpa* (Todaro, 1902) for *Cyclosalpa virgula* Vogt, 1854, and *C. komaii* Ihle and Ihle-Landenberg, 1936, and *Weelia* gen. nov., for *Salpa cylindrica* Cuvier, 1804. In addition, the subfamilies Cyclosalpinæ and Salpinæ are newly recognized here.

References included in the specific synonymies are as inclusive as possible since 1912. Additional citations prior to that date are given in detail by Ihle (1912). Only a few of the older reports (previous to 1893) have been examined, thus all citations in the synonymies previous to 1912 have been taken from Ihle unless stated otherwise.

Acknowledgments

Dr. R. W. Hiatt suggested the study and has offered his help whenever needed. I wish to express my thanks for his patient criticism of the investigation in all aspects. I wish also to state my thanks to Dr. L. D. Tuthill who helped solve many problems of a systematic nature and criticized other aspects of the

¹ Contribution No. 53, Hawaii Marine Laboratory. A portion of a thesis submitted to the Department of Zoology and Entomology, University of Hawaii, in partial fulfillment of the requirements for the degree of Doctor of Philosophy. Manuscript received August 6, 1953.

study. Especial thanks are due Dr. P. B. van Weel who informed me of the effectiveness of toluidin blue as a stain for salps.

Mr. O. E. Sette, in charge of the Pacific Oceanic Fishery Investigations of the United States Fish and Wildlife Service (referred to in the remainder of this report as POFI), kindly permitted me to use the plankton samples of POFI. In addition, Mr. J. E. King of POFI was helpful in the final judgment as to which plankton samples would be used, as well as in obtaining the samples.

The figure of *Thetys vagina* agg. (Fig. 23*b*) was drawn by Mr. James Park, illustrator of the Department of Zoology and Entomology, University of Hawaii.

MATERIALS AND METHODS

The animals used were taken from a large series of plankton captures made by POFI (principally from cruise 5 of the "Hugh M. Smith"). The area of capture extended from 27°N. to 5°S. and from 176°W. to 155°W.

The animals were studied by staining with toluidin blue. Apparently the idea of staining the animals has not been used by anyone previous to this report except Berner (1954), who used rose bengal.

Salps cannot be advantageously stained in an alcoholic stain, as alcohol dehydrates the test. Some water-soluble stains (such as rose bengal) were found to be rather effective, but they did not result in good differentiation between test and other body structures. P. B. van Weel suggested the use of toluidin blue, which he had used on salps as a vital stain and which, he had found, differentiated between body tissues and test of the living animal. It has proved a most important contribution to this study.

Toluidin blue can be mixed in any water medium, whether it contains formalin, is salty, or is fresh. The dry stain was sprinkled into the fluid until the latter became a deep blue or purple color. The most satisfactory strength is 0.15 gram stain to 500 cubic centimeters water. The animal was placed in the

stain from 5 to 30 minutes. While it was in the stain, a small pipette or hypodermic needle was used to inject stain through the mouth or cloacal opening in order to stain body tissues; this is an essential step of the staining process. When body muscles and other internal organs became rather dark, the animal was washed in a vessel containing clear water to remove excess stain. It was then ready for study, best done with a white background, but a black background or even removal from the water may be useful. There are, however, two disadvantages to the use of the stain: (1) it is not permanent in the preservative, and (2) the natural coloration of the animal becomes obscured. The many advantages of the stain, however, greatly outweigh these disadvantages.

Some salps, such as the solitary forms of *C. bakeri*, *C. floridana*, and *H. komaii*, require a different method than the one just described. In the first two species, the muscles are so delicate that they do not stain well at the usual concentration; in the latter species the test absorbs stain heavily, thereby obscuring structures beneath it. The animals were placed in clear water, *not* in the stain. Then a stain of 1 gram to 500 cubic centimeters of water was injected slowly into the body cavity until it was completely filled, and left until the muscles became dark. In this way, the test is not stained, but the body structures are.

Toluidin blue differentiates by staining the test pink and the body tissues varying degrees of blue. Thus the test and various organs of the body become completely visible and yet retain their transparency to a large degree.

Stiasny (1926) reported that the test is useful in combination with other structures, especially muscles, for distinguishing species. However, extensive examination of the stained tests shows that in the aggregate form there is often no basic type of test. It is apparently not as useful as he thought, as I found great variation in test structure of both solitary and aggregate forms.

In many species, the presence of depressions and elevations is entirely accidental, due probably to the convulsive contractions of the muscles at death. In my opinion the presence of elevations and depressions in a soft test (with the exception of distinct ridges and grooves) is in general without value as a character for species determination. There do seem to be a few exceptions, however, i.e., *Pegea confederata* and *Ritteriella amboinensis* agg.

The asymmetric nature of aggregate individuals of salps is shown not only in the arrangement of muscles, attachment organs, and end projections but also in the sculpture of the test when it is stiff and has permanent structures (Stiasny, 1926; Ihle, 1937-39).

In some species, such as *Thalia democratica*, there are two basic body forms: one has a relatively thick test, prominent ridges and grooves, and wide muscle bands; the other has a thin test, ridges weak or absent, non-permanent elevations and depressions, and narrow muscles.

Van Beneden and de Selys-Longchamps (1913) (*vide* Stiasny, 1926) and Stiasny showed that there had been entirely too much reliance on muscle arrangement for differentiating the various species. Nevertheless, muscle arrangement is one of the most important recognition features. In order to determine some species, however, it must be combined with other features.

MORPHOLOGY

With the exception of Traustedt (1885), Brooks (1893), van Beneden and de Selys-Longchamps (1913) (*vide* Brien, 1948), and Stiasny (1919, 1926), all investigators have described the test only incidentally, their work being primarily concerned with the muscular arrangements of the various species. The only considerable contribution to the knowledge of test structure was made by Stiasny (1926). As he showed, the great difficulty encountered in the study of the test is its almost complete agreement in refractive index with water.

Some salps have tests with ridges and grooves that can be seen under water, but the test of most shows little or no opacity. Hence, almost all investigators have completely disregarded the test in their researches. Traustedt (1885) and Brooks (1893) described the test in a few species, and Brooks recognized a basic plan in the test that fits some salps, especially the solitary forms. This plan was named Brooks' rule (Regel von Brooks) by Stiasny (1926), and he applied it to many forms. Stiasny also clarified the rule and stated it as follows:

... finden wir regelmässig in der Mitte der Dorsalseite eine (tiefe) Längsfurche, beiderseits begrenzt von vorspringenden kiel-ähnlichen Kanten, an den seiten des Mantels vorspringende scharfe Kanten oder Flügelartige Verbreiterungen; auf der Ventralseite ist die Testa dick, mit einem medianen und 2 lateralen Kielen.

Stiasny also set up a scheme of nomenclature for test structure which is followed here although some of his terms have been changed. The result is a combination of his terms, of those used by Delage and Hérouard (1898), and some additions. It is believed that the terminology used here is both clearer in meaning and easier for use in descriptions. The resulting scheme is shown in Figure 1.

The following terms are used to describe the test:

- test*—the outer tunic or covering over the epidermis
- mantle*—the epidermis and associated tissues; the term does not refer to the test
- ridge*—a distinct elongate bulge, triangular in cross section
- groove*—a distinct elongate, angular invagination
- elevation*—a rounded, elongate bulge
- depression*—a rounded, elongate invagination
- swelling*—a prominent, nonelongate, rounded bulge
- cavity*—any concavity of the internal surface of the test

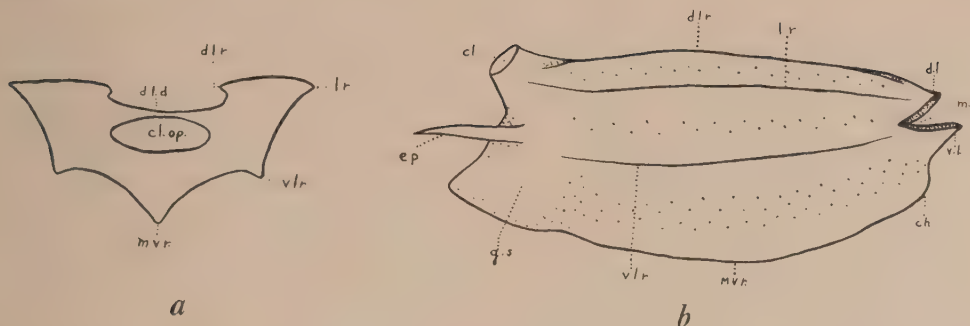


FIG. 1. Scheme of the test of a solitary form. *a*, End aspect (after Stiasny, 1926); *b*, lateral aspect (modified after Delage and Hérourard, 1898). *cb*, Chin; *cl*, cloacal opening; *dl*, dorsal lip; *dld*, dorsal longitudinal depression; *dlr*, dorsal limiting ridge; *ep*, end projections; *gs*, gut swelling; *lr*, lateral ridge; *m*, mouth; *mvr*, midventral ridge; *vl*, ventral lip; *vlr*, ventrolateral ridge.

chin—the swelling on the ventral anterior surface below the ventral lip

spine—a small, conical protrusion beyond the test margin

projection—a large protrusion of the test; it is never filamentous but may contain a mantle projection

tentacle—a filamentous protrusion of the test; it usually contains a mantle projection

sucker—a disc-like enlargement at the end of the mantle (epithelial) tube in the projections of some forms (e.g., *Thaliademocratica*, sol.)

Furthermore, when the terms “ridge,” “groove,” etc., are used, they always refer to longitudinal ridges and grooves unless stated otherwise.

The general morphology of salps is schematized in Figure 2 to identify structures in the remaining figures. Body muscles are designated by Roman numerals from anterior to posterior (M III = body muscle three), whereas mouth and cloacal muscles are designated by letters (A, B, C, and x, y, z, respectively). This notation follows that set up by Streiff (1908) as used by Ihle (1935, 1937–39), except cloacal muscles are denoted by lower-case letters to avoid confusion with body muscles.

In addition to those listed in Figures 1 and

2, the following abbreviations are used in the other figures: *ant*, Anterior; *bl.f*, blood-forming organ; *bm*, “baumförmiger Fortsätze”; *bv*, blood vessel; *cir.pr*, circular projection; *cl.fl*, cloacal flap; *cr*, crest (dorsal limiting ridge); *dle*, dorsal limiting elevation; *dlp*, dorsolateral projection (atrial palp); *d.ten*, dorsal tentacle; *el.c*, elaeoblast cavity; *em*, embryo; *f*, fold in bottom of pharynx; *hft*, attachment organ; *ho*, hook; *in*, independent muscle; *lo*, light organ; *lpp*, lateral posterior projection; *mdr*, middorsal ridge; *mvp*, midventral projection; *ob.gr*, oblique groove; *ob.r*, oblique ridge; *pa*, test patch; *ped*, peduncle; *pl.pr*, posterolateral projection (tentacle); *pr*, posterior ridge; *R*, right side; *rec*, rectum; *sn*, snout; *st.at*, attachment organ; *st.op*, opening for stolon; *tes*, testis; *tr.d*, transverse depression; *vle*, ventrolateral elevation; *vlp*, ventrolateral projection; *vr*, ventral ridge.

Most drawings in this paper do not show oral or cloacal muscles, as these are small and difficult to place correctly in a drawing of the whole animal. They are described and figured for most species by Streiff (1908), Metcalf (1918), Ihle (1935, 1937–39), and Thompson (1948).

It is probable that further study will show that the attachment organs are of considerable taxonomic importance. They are only incidentally described in this paper.

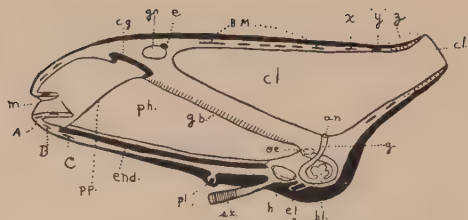


FIG. 2. Schematic median section of a solitary salp (after Ihle, 1935). A, Velum muscle; an, anus; B, lip muscle; bl, blind sac (caecum of gut); BM, body muscles; C, bow (intermediate) muscle; cg, ciliated groove (dorsal tubercle); cl, cloaca and its opening; e, eye; el, elaeoblast; end, endostyle; g, gut (intestine); gb, gill bar; gn, ganglion; h, heart; m, mouth; oe, esophagus; pb, pharynx; pl, placenta; pp, peripharyngeal band; st, stolon; x, first cloacal muscle; y, second cloacal muscle; z, third cloacal muscle (composed of a series of small sphincters).

KEY TO WORLD SPECIES AND REPRODUCTIVE FORMS OF SALPIDAE

1. Gonads present; stolon absent; eggs or embryos usually present. . . . aggregate (gregarious) form. 2
 Gonads absent; stolon usually present; eggs and embryos absent. . . . solitary (oozoid, asexual) form. 22
- 2(1). Intestine straight, anteriorly directed; one light organ present laterally between M II-III (there may be another between M III-IV) *Cyclosalpa pinnata*
 Intestine neither straight nor anteriorly directed; no light organ present. 3
- 3(2). Two posterior projections present, containing testis and a caecum, respectively. *Cyclosalpa bakeri*
 One or no posterior projection present. 4
- 4(3). Testis spherical. *Helicosalpa komaii*
 Testis not spherical. 5
- 5(4). Posterior appendage containing testis present. 6
 Posterior appendage containing testis not present. 7
- 6(5). Testis projects dorsolaterally within posterior test projection.
 *Helicosalpa virgula*

Testis projects ventroposteriorly within posterior swelling.

. *Cyclosalpa floridana*

- 7(5). Gut forms a broad loop with central space empty; a peduncle present.

. *Cyclosalpa affinis*

Gut either tightly looped or with central space filled; peduncle absent. 8

- 8(7). Some body muscles form complete rings. 9

No body muscles form complete rings. 10

- 9(8). Body muscles fused into a single unit dorsally and ventrally.

. *Brooksia rostrata*

Body muscles not fused into a single dorsal and ventral unit; however, M II and III are rings. . . *Ihleia magalhanica*

- 10(8). All body muscles interrupted dorsally. *Thetys vagina*

Some or all body muscles continuous dorsally. 11

- 11(10). M I interrupted dorsally.
 *Iasis zonaria*

M I continuous dorsally. 12

- 12(11). Four symmetrical attachment organs project from each side of body.

. *Pegea confoederata*

Attachment organs either asymmetrical or not projecting beyond test outline. 13

- 13(12). One elongate tentacle projects posteriorly from each lateroposterior angle of body. *Traustedia multitentaculata*

No elongate tentacle as above (short attachment organs may project laterally from the posterior region of *Thalia democratica* agg.) 14

- 14(13). Ventral lip sphincter 4 (Mb₃) interrupted. *Salpa fusiformis*

Ventral lip sphincter 4 continuous, if present. 15

- 15(14). Muscles arranged in groups of 3 and 2 dorsally. 16

- Muscles arranged in groups of 4 and 2, 4 only or 2 only dorsally. 18
- 16(15). Gut within a broad pointed or rounded median posterior projection; ciliated groove bears a ventral languet. 17
Posterior projection not containing gut; ciliated groove without languet.
..... *Weelia cylindrica*
- 17(16). M III is formed of 8 or 9 fibers (Apstein, 1906a). *Thalia longicauda*
M III is formed of 3 fibers (Apstein, 1906a). *Thalia democratica*
- 18(15). M II extends beyond endostyle to between M V–VI of opposite side.
..... *Ihleia punctata*
M II not as above. 19
- 19(18). Posterior projection extends beyond cloacal opening. 20
Posterior projection does not extend beyond cloacal opening.
..... *Metcalfina hexagona*
- 20(19). Independent muscle small, inconspicuous; M I–II narrowly fused dorsally; spaces between transverse ribs of gill bar less than 0.5 width of bar.
..... *Salpa maxima*
Independent muscle large, conspicuous; M I–II widely fused dorsally; spaces between transverse ribs of gill bar greater than 0.5 width of bar. 21
- 21(20). Dorsal lip sphincter 1 (M A₁) interrupted middorsally.
..... *Ritteriella picteti*
Dorsal lip sphincter 1 continuous middorsally. *Ritteriella amboinensis*
- 22(1). Intestine accompanies gill bar. 23
Intestine does not accompany gill bar. 28
- 23(22). Ventral longitudinal muscle present. 24
Ventral longitudinal muscle absent. 25
- 24(23). A single dorsal longitudinal muscle present, connecting M I with M x on each side. *Helicosalpa komaii*
- Two dorsal longitudinal muscles present, connecting M I with M VI on each side. *Helicosalpa virgula*
- 25(23). M I–IV fused ventrally into a single mass. *Cyclosalpa floridana*
M I–IV not fused ventrally. 26
- 26(25). Three to five light organs present on each side of body. 27
Not more than one light organ present on each side of body. *Cyclosalpa affinis*
- 27(26). M VI forming 2 anteriorly directed dorsal longitudinal muscles.
..... *Cyclosalpa bakeri*
M VI forming one fused, anteriorly directed dorsal longitudinal muscle, or none. *Cyclosalpa pinnata*
- 28(22). A muscular snout projects anteriorly beyond mouth opening.
..... *Brooksia rostrata*
No muscular snout projects anteriorly. 29
- 29(28). Body muscles interrupted dorsally. 30
Body muscles continuous dorsally. 31
- 30(29). A long projection extending posteriorly from both posterolateral angles of body; test spiny. *Thetys vagina*
No such projections present; test smooth. *Iasis zonaria*
- 31(29). Some body muscles form complete rings. 32
All body muscles interrupted ventrally. 36
- 32(31). Longitudinal muscles present on each side of body, internal to body muscles. *Ihleia punctata*
Longitudinal muscles absent. 33
- 33(32). A long projection extending posteriorly from each posterolateral surface of body. 34
No such projections present. 35
- 34(33). M I–III and IV–V forming groups dorsally. *Thalia democratica*

- All body muscles separate, parallel (Traustedt, 1885) *Thalia longicauda*
- 35(33). Not more than first four body muscles forming complete rings
 *Ritteriella amboinensis*
 M I–VI forming complete rings (Thompson, 1948) *Ihlea magalhanica*
- 36(31). Intestine straight, extended posteriorly *Ritteriella picteti*
 Intestine coiled, not extended 37
- 37(36). Projections of test or tentacles extending beyond body outline 38
 No projections of test extending beyond body outline 39
- 38(37). Two posterior projections present; 9 to 13 body muscles present, asymmetrical *Metcalfina hexagona*
 No posterior projections but with two to many tentacles; body muscles few (5), symmetrical
 *Traustedtia multitentaculata*
- 39(37). Four body muscles present
 *Pegea confoederata*
 More than 4 body muscles present . . 40
- 40(39). Elaeoblast or its cavity present in mature specimens; ciliated groove forming a loop *Salpa maxima*
 Elaeoblast present only in embryos; ciliated groove simple in immature specimens 41
- 41(40). M I–IV converging to form a group *Weelia cylindrica*
 M I–III and VIII–x converging, or are parallel *Salpa fusiformis*

Family SALPIDAE

The definition of the family by Ihle (1935) is followed here chiefly.

Planktonic Thaliacea with main body axis longitudinal, covered with a transparent test. Mouth opening anterior, cloacal opening posterior, dorsal or terminal. Body musculature consists of usually ventrally interrupted mus-

cles but may include complete rings or dorsally interrupted muscles as well. Special mouth and cloacal musculature present. Pharyngeal and cloacal cavities separated by a "gill bar" lying between two large gill slits; gill bar extending from anterodorsal surface to esophagus located posteroventrally. An alternation of generations exists between the sexual blastozoid (aggregate or gregarious form) and the asexual oozoid (solitary form). The oozoid bears ventrally a proliferating stolon on which the blastozooids arise. The blastozoid produces one or several embryos on the cloacal wall which become oozoids.

The family Salpidae consists of two distinct groups of genera. I propose to give these groups the status of subfamily: the Cyclosalpininae including *Cyclosalpa* and *Helicosalpa*, the former being the type genus, and the Salpininae including all other genera of the Salpidae, *Salpa* being the type genus.

CYCLOSALPINAE subfam. nov.

The subfamily Cyclosalpininae may be distinguished by the following characteristics: (1) in the solitary form, the intestine accompanies the gill forward, being united with it over most of its length; (2) there are light organs present in all solitary forms except *C. affinis*, and here one is probably present (see description); (3) in the aggregate form, the gut is either an extended tube or a loosely formed loop, never a compact "nucleus"; (4) the aggregate forms are attached by a single peduncle or by a single large attachment process.

Genus CYCLOSALPA Blainville, 1827

Solitary form with six body muscles, gregarious form with four. In the solitary form longitudinal muscles absent or, if present, no, continuous with M I. Intestine coursing obliquely with gill bar in the solitary form, but not forming a rectum. Intestine either straight or forming an open circle in the aggregate form. Only one attachment organ, the pe-

duncle, present in the aggregate form. Body muscles penetrating into peduncle. Groups of blastozoids forming whorls on stolon.

Four species: *Cyclosalpa pinnata* (type), *C. affinis*, *C. floridana*, and *C. bakeri*.

***Cyclosalpa pinnata* (Forskål) 1775**

Fig. 3a-d

- Salpa pinnata* Forskål, 1775: 113.
Biphora pinnata Bruguière, 1789: 180.
Salpa pelagica [?] Bosc, 1802: 181.
Salpa cristata Cuvier, 1804: 366.
Salpa thalia [?] Lamarck, 1816: 119.
Salpa caudata [?] Lamarck, 1816: 119.
Salpa (Cyclosalpa) pinnata Blainville, 1827: 108;
 Metcalf, 1918: 9; Sewell, 1926: 68; Stiasny,
 1926: 414.
Salpa cyanea [?] Chiaje, 1828: 63.
Salpa proboscidalis Lesson, 1830: 95.
Salpa mucosa [?] Costa, 1839: 225.
Orthocoela pinnata Macdonald, 1864: 181.
Cyclosalpa pinnata Herdman, 1888: 87; Ihle,
 1935: 527-529; Tokioka, 1937: 219;
 Thompson, 1948: 103.
Cyclosalpa polae Sigl, 1912a: 66; 1912b (*vide*
 Ihle and Ihle-Landenberg, 1937); Fedele,
 1926, 1933 (*vide* Ihle and Ihle-Landenberg,
 1937); Ihle and Ihle-Landenberg, 1937: 1.
Cyclosalpa bakeri Bomford, 1913: 243.
 [non] *Cyclosalpa bakeri* Ritter, 1905: 54.
Salpa (Cyclosalpa) pinnata polae Metcalf, 1918:
 26; Sewell, 1926: 68; Komai, 1932: 69.
Cyclosalpa pinnata polae Ihle, 1935: 527-529.
Cyclosalpa pinnata var. *polae* Tokioka, 1937:
 220.

SOLITARY FORM: Four specimens examined with length range of 4-12 mm. (Fig. 3c,d). **Test:** Rather thin, glutinous, without definite elevations or depressions. Median dorsal ridge described by Stiasny (1926) absent as are anterior "ventral languets" shown by Metcalf (1918). **Muscles:** Six body muscles, each interrupted dorsally and ventrally; oral muscles touching M I. **Ciliated groove:** An arched U in dorsal view, but may be sinuous or convoluted according to various investigators.

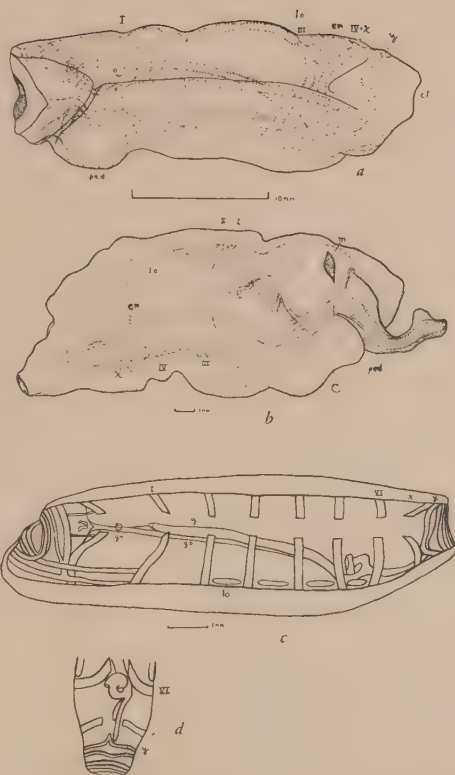


FIG. 3. *Cyclosalpa pinnata*. a, Aggregate form, left dorsal side; b, aggregate form, right dorsal side; c, solitary form, left side; d, solitary form, ventral view of cloacal region.

Viscera: Esophagus opening between M VI and x on right side, connecting to intestine which accompanies gill antero-obliquely; at junction of intestine and esophagus, two caeca projecting posteriorly, the left one almost twice the length of the right one; light organs four on each side, between muscle bands II-x (five according to most investigators, but Sewell, 1926, found only four—none between I-II—and this is also true of POFI specimens).

AGGREGATE FORM: Four specimens examined with length range of 11-31 mm. (Fig. 3a,b). **Test:** Thin and flabby, far separated from mantle except at region of mouth and cloacal openings; glutinous; no definite

elevations or depressions; peduncle long in small (*C. p. polae*?) specimens (Fig. 3*b*), much shorter in largest specimen (Fig. 3*a*). *Muscles*: Four body muscles; M I-II fused dorsally, III, IV, and x approaching or fusing dorsally; mouth muscles joining M I; bow muscles (C) forming anterior peduncle muscles on each side, M I and II fusing ventrolaterally to form posterior peduncle muscles. Thus, a total of four peduncle muscles present. *Ciliated groove*: Simple or U-shaped, located vertically. *Viscera*: Esophagus opening at level of junction of M III-IV-x; a single, posteriorly directed caecum, intestine coursing anteriorly beneath endostyle, anus opening at region of M II-III, but in larger specimen at region of M I; testis prominent, longitudinally plicated, arising at junction of esophagus and intestine, accompanying intestine anteriorly, opening by small duct slightly posterior to anus; embryo near M III or between M III-IV dorsally; one light organ on each side between M II and III—there may be two, as shown in Fig. 3*a* and as shown by Ihle (1910), Komai (1932), and Tokioka (1937); examples previously described with two pairs of light organs, as the present specimen, always large (length of specimen, 28 mm.), so this condition probably due to age.

The form (species, subspecies, variety) *polae* has been distinguished from *C. pinnata* chiefly by the following characteristics in the gregarious form (Ihle and Ihle-Landenberg, 1937); length of body, length of peduncle, relationships of M III and IV dorsally, shape of ciliated groove, eye, caecum (blind sac), and position of anus. There are evidences, however, chiefly from Sewell (1926), that this form is not distinct from *C. pinnata*. The separation dorsally of M III and IV is found in *C. pinnata* as well as in animals fitting the description of *C. polae* (Metcalf, 1918; Sewell, 1926; Komai, 1932). The ciliated groove intergrades between the form *polae* and the type (Sewell, 1926). The solitary form of *C. polae* is distinguished (Sigl, 1912*a*) by the middorsal fusion of the two M VI and their continuance

as a band forward. This character apparently intergrades but should receive further study. Sewell (1926) stated:

Had I been dealing solely with examples of the aggregated zooid I should have had no hesitation in referring this form to the sub-species *polae* but, as I have already shown, the asexual generation [of the Indian form] must be referred to *C. pinnata*. It is impossible, therefore, to distinguish *Cyclosalpa polae* from *C. pinnata* even as a sub-species, and much less, as Sigl originally claimed, as a species.

Ihle and Ihle-Landenberg (1937), however, critically studied specimens of the aggregate zooid of both forms and concluded that the two forms should be considered distinct species, as Sigl (1912*a*) had regarded them.

I have had only typical specimens of the solitary zooid of *C. pinnata* and thus can add nothing which might help settle this problem. The aggregate zooids of the POFI collections, however, show intergradation in the dorsal separation of M III-IV and structure of the ciliated groove. Tentatively, I follow Thompson (1948) in regarding the form *polae* as simply showing differences attributable to changes occurring with increasing size and believe that its recognition as a subspecies or species is probably not justified. Doubtless, the answer to the problem lies in a study of various-sized solitary forms.

An embryo was found in a collection containing aggregate forms that fit the description of *C. polae* (Fig. 3*b*). This embryo, however, is evidently a typical *C. pinnata* as the two M VI do not fuse dorsally. It was not attached to its mother, so I cannot relate it directly to the form *polae*.

Cyclosalpa affinis (Chamisso) 1819

Fig. 4 *a*, *b*

Salpa affinis Chamisso, 1819: 11.

Cyclosalpa affinis Blainville, 1827 [*vide* Ritter, 1905]; Ihle, 1935: 527-529; Tokioka, 1937: 221; Thompson 1948: 108.

Salpa pinnata var. [?]Quoy and Gaimard, 1834: 582.

Salpa chamissonis Brooks, 1893: 376.

Salpa (Cyclosalpa) affinis Apstein, 1894b: 4;
Metcalf, 1918: 27; Sewell, 1926: 74; Komai,
1932: 70.

SOLITARY FORM: One specimen examined with length of 54 mm. (Fig. 4a). *Test*: Thin, glutinous, attached at mouth and cloacal opening; no definite elevations or depressions. *Muscles*: Six body muscles: M I and II interrupted dorsally and ventrally, M III–VI interrupted ventrally, continuous dorsally; x sending one branch anteriorly (broken in this specimen) which is continuous with posterior branch of M VI; x continuing far ventrally; x and y converging laterally but not touching; M I joining mouth muscles. *Ciliated groove, ganglion and eye*: Ganglion and eye anterior to M I, just above anus; ciliated groove far anterior to them, highly convoluted. *Viscera*: Esophagus forming a spiral at ventral level of M VI and x; a single posterior caecum (actually double, appearing single, according to Komai, 1932) connecting to intestine which courses antero-obliquely with gill; anus opening just anterior to M I; gill ending anterior to M C; a large oval body located on each side between M IV and V. It is conspicuous with stain and probably is a light organ (this is not mentioned in past descriptions).

AGGREGATE FORM: Three specimens examined with length range of 18–33 mm. (Fig. 4b). *Test*: Closely attached at mouth, cloacal opening, on peduncle and intestine (Metcalf, 1918, figures it as very loose on latter two structures); test with no definite elevations or depressions, glutinous, thin, may be far separated from mantle; peduncle short, broad. *Muscles*: Four body muscles; all interrupted ventrally, continuous dorsally and separated from one another except IV and x; M I joining with mouth muscles; M C forming anterior peduncle muscles, posterior peduncle muscles independent; total of four muscles in peduncle, two anterior and two posterior; M I sending off two anterior branches; x and

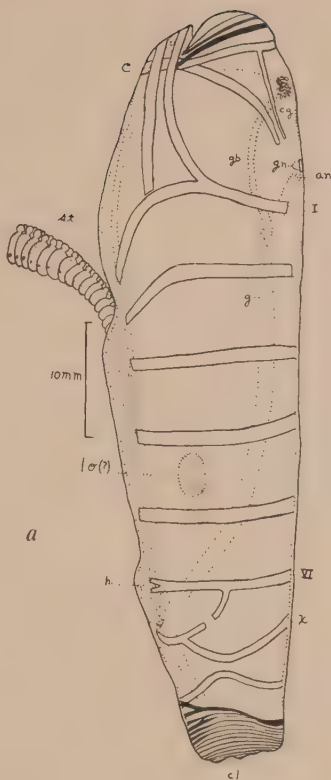


FIG. 4. *Cyclosalpa affinis*. a, Solitary form, left side; b, aggregate form, right side.

y connected by a laterodorsal branch. *Ciliated groove*: Anterior to M I, highly convoluted. *Viscera*: Gut a large open loop, forming a posteroventral evagination beyond body outline; testis contained in gut loop; embryo on right side between M III and IV; no light organs.

Cyclosalpa floridana (Apstein) 1894

Fig. 5a, b

Cyclosalpa dolicosoma-virgula Traustedt, 1893: 5.

[non] *Salpa virgula* Vogt, 1854: 11.

Salpa floridana Apstein, 1894b: 9.

Cyclosalpa floridana Brooks, 1908: 75 [fide Sewell, 1926]; Ihle, 1935: 527-529; Ihle and Ihle-Landenberg, 1935: 21; Thompson, 1948: 111.

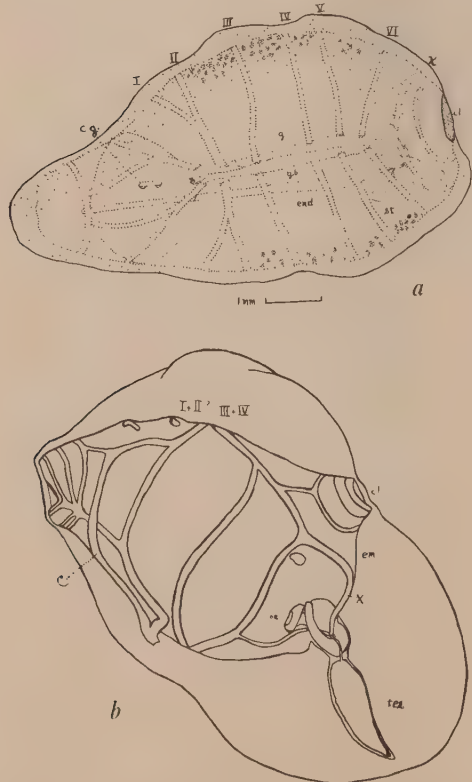


FIG. 5. *Cyclosalpa floridana*. a, Solitary form, dorsal surface; b, aggregate form, left side (modified after Metcalf, 1918).

Salpa (Cyclosalpa) floridana Metcalf, 1918: 32; Sewell, 1926: 72.

[non] *Cyclosalpa floridana* Apstein 1906a: 248; 1906b: 162.

SOLITARY FORM: One specimen examined with length of 8 mm. (Fig. 5a). *Test*: Rather thick, glutinous; with no definite elevations or depressions; rather far separated from mantle; attached at mouth and cloacal opening. *Muscles*: All six interrupted dorsally, ventrally continuous and fused into a single mass; M I-II joining dorsally; M I joining mouth muscles. *Ciliated groove*: Simple crescent with points turned ventrally. *Viscera*: Esophagus joins intestine ventrally at level of M VI; single, ventral caecum projecting from point where intestine courses antero-obliquely with gill; anus opening at level of M II (Metcalf shows this anterior to M I just under ganglion); light organs patchy masses of cells between the following muscles on each side: II-III-IV-V-VI.

AGGREGATE FORM: Two specimens examined, with lengths of 2.5 and 4 mm.

As both POFI specimens are in very poor condition, the following description is based on Metcalf, as is the figure (Fig. 5b). *Test*: Thin, far separated from body except at mouth and cloacal openings; forming a large bulge or swelling posteroventrally for testis and gut. *Muscles*: Three body muscles; M I joining mouth muscles and, with M C, forming peduncle muscles; M I-II and III-IV-x converging dorsally; M III-IV-x joining dorsally, converging ventrally; all muscles continuous dorsally and ventrally; x joining y by a bridle piece which extends over gut. *Ciliated groove*: Simple crescent. *Viscera*: Intestine forming a close loop, anus opening on left behind esophageal opening; testis large, projecting posteroventrally from gut; embryo located between M IV and x laterally.

Cyclosalpa bakeri Ritter (1905)

Fig. 6a-c

Cyclosalpa bakeri Ritter, 1905: 54; Ihle, 1935:

527–529; Thompson, 1948: 114; Tokioka, 1951: 183.

Cyclosalpa floridana Apstein, 1906a: 248; 1906b: 162.

[non] *Salpa floridana* Apstein, 1894b: 9.

Salpa (Cyclosalpa) bakeri Metcalf, 1918: 37.

SOLITARY FORM: One specimen examined with length of 34 mm. (Fig. 6a, b). *Test:* Thin, flabby, glutinous; closely attached to mantle; no definite elevations or depressions; pear-shaped with posterior end smallest. (This does not agree with the figure of Metcalf, which shows the test far separated from the mantle.) *Muscles:* Six body muscles, of which M I joins mouth muscles laterally and ventrally; all body muscles and x dorsally interrupted (Ritter, 1905, and Metcalf, 1918, say that x is sometimes complete dorsally), all except x ventrally interrupted (the above-named authors say that x is also ventrally interrupted); ventrally, y fusing with its fellow of the opposite side, extending shortly anteriorly between the gut caeca; dorsally M VI extending anteriorly almost to level of M II (to level of M IV according to Ritter and Metcalf); left and right anterior dorsal extensions of M VI remaining distinct. *Ciliated groove, ganglion and eye:* Ciliated groove forming an open U with left horn extended farther anteriorly; ganglion and eye just anterior to M I. *Viscera:* Esophagus opening at region of M VI ventrally; intestine accompanying gill antero-obliquely, anus opening behind eye level; two equally long, laterally compressed caeca projecting posteriorly; stolon held within a mantle tube which opens at level of M I–II; light organs large and distinct, four on one side, three on other in POFI specimen; each located laterally over a body muscle (previous reports show five large light organs and one small anterior one, between body muscles).

This animal most closely resembles the *polae* form of *Cyclosalpa pinnata* (according to the description of Sigl, 1912a, and the statement of Thompson, 1948). It can be distinguished from that form by the nonfusion of the two

M VI dorsally, and by the fact that in *C. bakeri* the caeca are of equal length, whereas in *C. pinnata* they are unequal.

AGGREGATE FORM: Eight specimens examined with length range of 7–9 mm. (Fig. 6c). *Test:* No definite elevations or depressions; flabby, thin except around posterior projections; either closely applied or far separated from mantle; attached at cloacal siphon and mouth; two prominent posterior end projections of thicker test present; the whorl of zooids released from the stolon covered by an outer coat of test, including seven zooids both in my specimens and in Thompson's figure (1948, pl. 42). *Muscles:* Two main muscle groups dorsally; each dividing laterally into several branches; anterior group joining mouth muscles; peduncle muscles three on each side, anterior one from M C, lateral one from M I–II, and a short posterior one from M III which extends anteroventrally toward peduncle; muscles of posterior muscle mass continuous ventrally; muscle structure asymmetric. *Ciliated groove, ganglion and eye:* All anterior to M I; ciliated groove forming a crescent rather far anterior to ganglion and



FIG. 6. *Cyclosalpa bakeri*. a, Solitary form, dorsal aspect; b, solitary form, ventral aspect (a and b schematic; length of animal, 34 mm.); c, aggregate form, left side.

eye; latter just in front of M I, prominent. *Viscera*: Gut forming posterior loop at base of posterior projections beyond body margin; anus opening at esophageal level; testis occupying left posterior projection; a caecum from the gut plus a smaller "problematic" organ, considered by Metcalf to be probably homologous with the same organ (=blood-forming organ) of *Ritteriella*, occupying the right posterior projection; embryo located at region of posterior muscle mass on right side.

Genus *HELICOSALPA* Todaro, 1902

I have not seen the report of Todaro (1902) establishing this genus. Ihle (1935) stated in regard to Todaro's report, "Durch die starke Enantiomorphie, durch das Fehlen einer ringförmigen Anordnung der Blastozöoide in der Kette und durch die eigentümlichen Haftflächen weicht *Cyclosalpa virgula* (Vogt) so bedeutend von den anderen Arten ab, dass Todaro (1902) diese Art zur selbständigen Gattung *Helicosalpa* rechnete." Ihle did not follow this classification, considering the species *C. virgula* to agree so closely with the other cyclosalpas in muscle arrangement and structure of gut that he thought it should not be separated from them.

After careful examination of the species *H. virgula* and *H. komaii*, however, I am of the opinion that they are quite different from the species of *Cyclosalpa*; thus I agree with Todaro (1902). As *Helicosalpa virgula* was at that time the only known species of the genus, it must be considered the type.

The genus may now be characterized as follows.

1. There are two distinct gregarious forms produced on the stolon, the dextral and the sinistral individuals. Whorls are not produced on the stolon. Mirror imagery is shown in the arrangement of attachment organs, musculature, tentacle over the ciliated groove, the ciliated groove, testis, and posterior projection (*H. virgula*), eye, mouth, and cloacal siphon. Other variations in the two forms,

although not mirror imagery, are the position of the testis and posterior projection (*H. komaii*), embryo, gut, and anus ("primary asymmetry" of Komai, 1932; the mirror imagery is called "secondary asymmetry" by him). In a few other species of Salpidae (for example, *Brooksia rostrata* and *Ihleia punctata*) asymmetry occurs, but this apparently is secondary asymmetry.

2. There is no peduncle, only a blunt attachment organ by which the gregarious forms attach to the stolon. The body muscles do not enter this process as do the peduncle muscles of *Cyclosalpa*.

3. The solitary form possesses dorsal and ventral longitudinal muscles which are continuous with M I; the dorsal longitudinal muscles are paired (*H. virgula*) or united (*H. komaii*). The ventral longitudinal muscles are always paired; they are distinct from most transverse muscles (*H. virgula*) or joined by all transverse (body) muscles (*H. komaii*).

4. The anus of the solitary form is turned widely posteriorly from the anterodorsal region of the gill bar, forming a rectum.

The nearest known relative of *Helicosalpa virgula* and *H. komaii* is probably *Cyclosalpa bakeri*. Metcalf (1918) included *H. virgula* and *C. bakeri* in his group *Cyclosalpa asymmetricales* but did not attain a phylogenetically accurate division, stating: "The division of the subgenus into *Cyclosalpa symmetricales* and *Cyclosalpa asymmetricales*, while truly descriptive of the existing conditions, does not represent accurately degrees of relationship, for *Cyclosalpa bakeri*, an asymmetrical form, finds its nearest relative in *C. floridana*, an aberrant member of the group *symmetricales*."

The separation of *H. virgula* and *H. komaii* into a separate genus is considered phylogenetically valid, distinguishing them from the cyclosalpas.

Helicosalpa virgula (Vogt) 1854

Fig. 7a-d

Salpa virgula Vogt, 1854: 11.

Salpa dolicosoma Todaro, 1883: 41.

Salpa dolicosoma-virgula Traustedt, 1885: 360.

Helicosalpa virgula Todaro, 1902: 405.

Cyclosalpa virgula Apstein, 1906b: 161; Ihle, 1935: 527-529; Ihle and Ihle-Landenberg, 1936: 274; Thompson, 1948: 118.

Salpa (Cyclosalpa) virgula Streiff, 1908: 15; Metcalf, 1918: 43; Sewell, 1926: 73; Stiasny, 1926: 418.

[non] *Cyclosalpa dolicosoma-virgula* Traustedt, 1893.

[non] *Salpa (Cyclosalpa) virgula* Komai, 1932: 70.

SOLITARY FORM: One specimen examined with length of 141 mm. (Fig. 7*a,b*). **Test:** The test of this specimen is relatively huge compared with the body. Volumetric measurements were made by water displacement: the body measured 10 milliliters, whereas the test measured 148 milliliters. This great difference in volume has not been reported before, thus perhaps it is only an anomaly. Test globular, gelatinous, thick and flabby; slightly glutinous; formed of an outer thin membranous layer and a thick inner gelatinous layer; loosely attached to the body by a few fine strands of test tissue; without permanent elevations or ridges. Posterior languets shown by Metcalf (1918) not present in POFI specimen, but a pair of short test projections present at the cloacal region. **Muscles:** M I and VI are continuous dorsally on each side, forming two dorsal longitudinal muscles; M I extending posteriorly on ventral surface forming two ventral longitudinal muscles that end at region of stolon extrusion; M V interrupted dorsally, extending ventrally almost to stolon level as an anteriorly directed longitudinal muscle, thus almost meeting the posteriorly extended M I; M II, III, IV, and x dorsally and ventrally interrupted; M I joining mouth muscles. The close relationship of this species and *H. komaii* is evident from the similarity of muscle structure. It can easily be distinguished from it, as *H. virgula* possesses two dorsal longitudinal muscles rather than

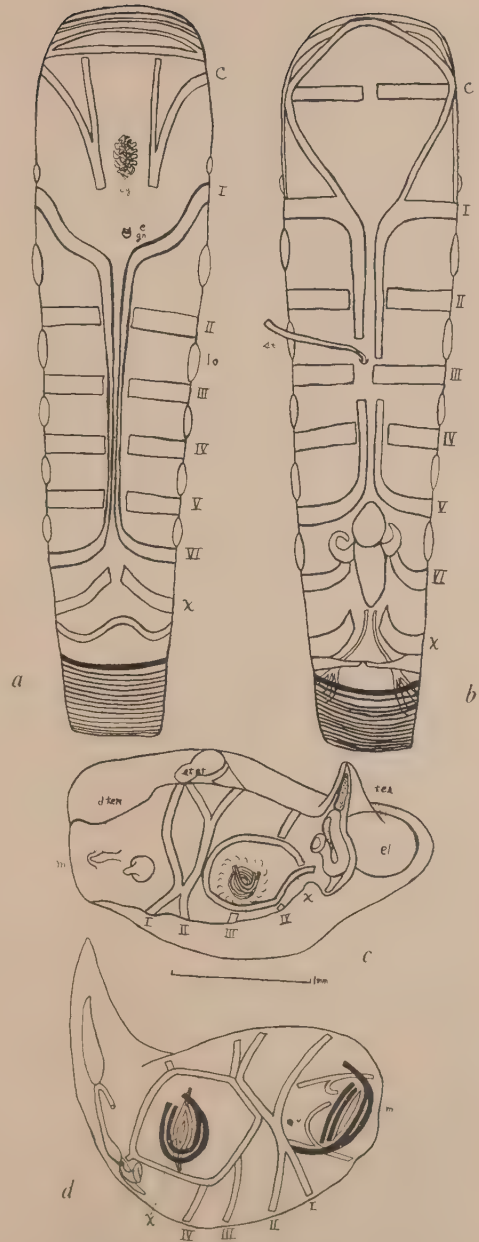


FIG. 7. *Helicosalpa virgula*. *a*, solitary form, dorsal aspect; *b*, solitary form, ventral aspect (*a* and *b* schematic, not showing the test; length, 141 mm.); *c*, aggregate form, sinistral individual from stolon, dorsal aspect; *d*, aggregate form, dextral individual, dorsal aspect (after Ihle, 1937-39, modified from Streiff, 1908).

one, and the ventral longitudinal muscles of *H. virgula* are not continuous (Streiff, 1908, however, represented them as continuous). In addition, the ventral ends of M II-IV remain distinct from longitudinal muscles in *H. virgula*. *Ciliated groove, ganglion and eye*: Ciliated groove highly convoluted, located at level of dorsoposterior extensions of M C; ganglion and eye at level of dorsal longitudinal muscles. *Viscera*: Gut large, bearing two caeca; intestine extending obliquely with gill, turning posteriorly at level of M I; stolon extruding from test at level of M III; six light organs on each side between body muscles from I to VI; additional small light organ anterior to M I (Streiff, 1908, Metcalf, 1918, and Stiasny, 1926, show a single continuous light organ extending from M I to M VI on each side; the photograph by Thompson, 1948, also shows a continuous light organ on each side; evidently, there is considerable variation in their location and structure).

AGGREGATE FORM: Only stolonetic individuals were studied with length of 3 mm. (Figs. 7c,d).

The aggregate forms of this species and *Helicosalpa komaii* are the most asymmetric of all the salps. The two types of aggregate individuals that are produced, dextral and sinistral, are described separately.

Dextral individual (Fig. 7d): This has been figured by Streiff (1908) and Metcalf (1918). In addition, Streiff described the sinistral individual, but Metcalf apparently had only dextral individuals for study. Test thick and firm with a bulbous swelling around elaeoblast and a large pointed projection containing part of gut and testis projecting dorso-laterally toward anterior left side of body; anus directed toward right; eye turned slightly to right of mid-line of body, as is the cloacal opening; four body muscles; x prominent, encircling cloaca, separating the two parts of M IV; dorsal tentacle projecting over ciliated groove to left of and anterior to ganglion.

Sinistral individual (Fig. 7c): Test similar to above, except projection containing gut and

testis directed to right; anus directed toward left; ganglion and eye slightly to left of mid-line of body, as is cloacal opening; muscles the mirror image of dextral individual; dorsal tentacle over ciliated groove projecting anteriorly and slightly to right of ganglion.

Helicosalpa komaii

(Ihle and Ihle-Landenberg) 1936

Fig. 8a-f

Salpa (*Cyclosalpa*) *virgula* Komai, 1932: 70.

[non] *Salpa virgula* Vogt, 1854: 11.

Cyclosalpa komaii Ihle and Ihle-Landenberg,

1936: 274; 1938b: 609; Tokioka, 1937: 221.

Cyclosalpa virgula Fedele, 1937: 448, 525 (*vide* Ihle and Ihle-Landenberg, 1938b).

[non] *Salpa virgula* Vogt, 1854: 11.

SOLITARY FORM: One specimen examined with length of 94 mm. (Komai's specimen was 230 mm. long, making this the largest of all known salps.) (Fig. 8a-d.) *Test*: Thick, flabby, strongly attached to mantle by numerous fine strands of test material; a prominent, nonserrated, middorsal ridge present on anterior half of test; without other permanent elevations or depressions; test composed of a thin outer layer and a thicker inner gelatinous layer; inner layer opaque (staining makes it more opaque, so should be used only with caution). Komai (1932) stated, "The test is thin and soft." I presume that he examined only the outer surface, which appears without dissection to be thin and rather far separated from the mantle by the inner gelatinous layer. *Muscles*: Six body muscles; x and y branched (Komai's figure, 8c of this report, shows y as a nonbranched muscle); mouth musculature including the large M C that approaches or touches M I dorso-laterally, passes backward ventrally as the ventral longitudinal muscle; two large sphincters of the dorsal lip (according to Komai, one large posterior and three small anterior ones) appearing to fuse laterally with two sphincters of the ventral lip, then continuing posteriorly as a dorsal retractor to the outside

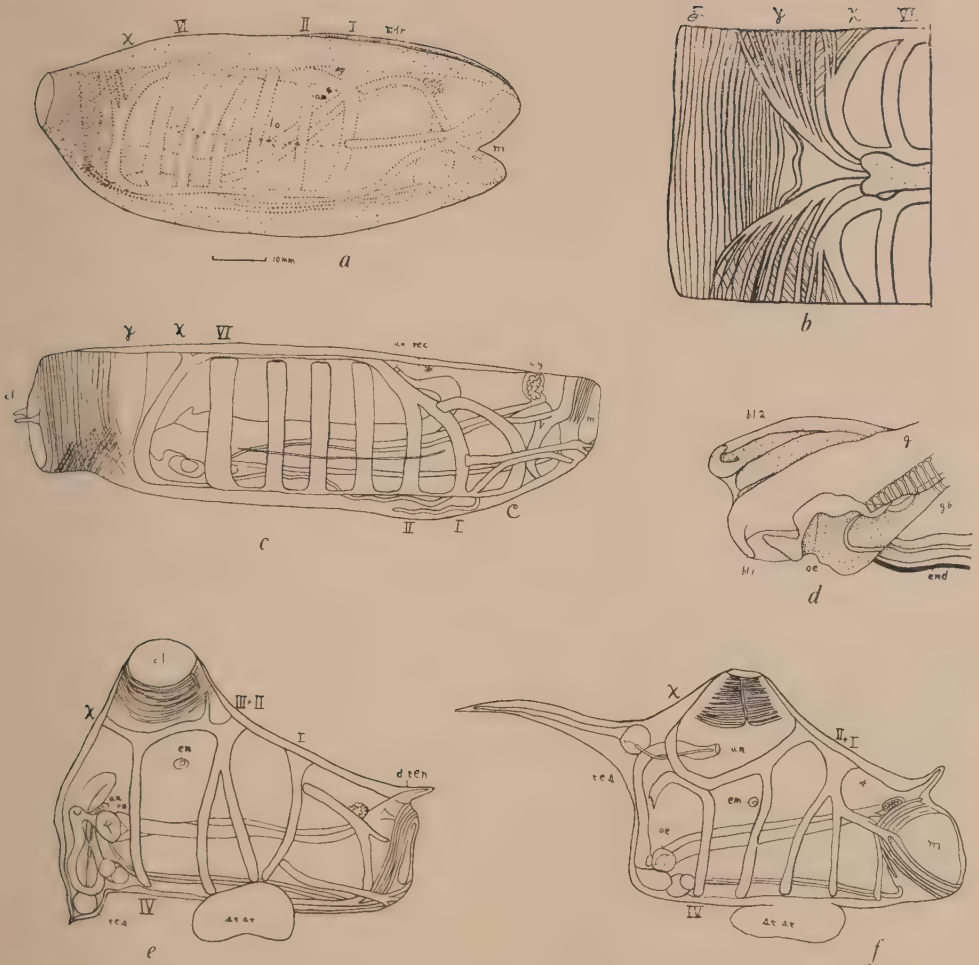


FIG. 8. *Helicosalpa komaii*. *a*, Solitary form, right side; *b*, solitary form, inside view of ventral cloacal region; *c*, solitary form (230 mm.), right side (after Komai, 1932); *d*, solitary form, posterior part of gut, right side (blind sac 2 has been turned slightly dorsad); *e*, aggregate form (about 50 mm.), sinistral individual, right side; *f*, aggregate form (about 70 mm.), dextral individual, right side. (*e* and *f* after Komai, 1932).

of M I, and as a ventral retractor which courses with M C as part of the ventral longitudinal muscle. Komai shows the dorsal retractor muscle formed only by ventral lip sphincters 1 and 2, the ventral retractor muscle formed by ventral lip sphincter 3. The specimen before me is rather mutilated anteriorly, so my description perhaps is wrong in some details. M I-II continuing dorsally as unpaired dorsal longitudinal muscle join-

ing x; x forming ventral longitudinal muscle (paired) which receives contributions from all body muscles as well as ventral retractor and M C of mouth region; there is thus a continuous rectangular muscle band which includes parts of all the major muscles of this animal. *Ciliated groove, ganglion and eye*: Ciliated groove highly convoluted, located anteriorly at level of M C; ganglion and eye at level of M I-II, just over rectum. *Viscera*:

Intestine elongate, coursing obliquely dorsad with gill, separating from it at level of M I forming a prominent posterior bend (rectum); forming two prominent caeca posteriorly which project equally posteroventrally in the POFI specimen, whereas Komai's figure shows one caecum projecting dorsoanteriorly, the other posteroventrally; stolon passing anteriorly in sinuous course, turning posteriorly just in front of M I (from Komai; the POFI specimen has no stolon); light organ composed of sparse masses of cells from M I-VI on each side of body.

AGGREGATE FORM: As no specimens of this form have been examined, the description follows those of Komai (1932) and Tokioka (1937). Length range of known specimens (Komai) 20-55 mm. without projections.

Dextral individual (Fig. 8f): Body ovoid, texture soft; one long posterior projection present; a cushion-shaped attachment organ on left ventral surface; atrial opening dorsal, tubular; musculature closely similar to that of *H. virgula*; gut forming open U-shaped loop at base of posterior projection; esophagus and left ventral caecum directed anteriorly; intestine extending dorsally, rectum bending anteriorly; small right caecum protruding to the right; testis spherical, located posterior to gut at base of posterior projection; a "whitish core" extending from testis to rear of posterior projection (considered by Komai probably homologous to the blood-forming organ of *Ritteriella*); ciliated groove highly convoluted; a prominent horn-like process borne dorsoanteriorly over ciliated groove.

Sinistral individual (Fig. 8e): Musculature the mirror image of that of dextral individual; attachment organ on right ventral surface; horn-like projection over ciliated groove extending dorsally toward right; posterior projection short, forming a blunt cone; esophagus and anus close to one another, located dorsally; esophagus coursing posteriorly, intestine bending ventrally, then dorsally and opening on left side of esophagus; left caecum large, opening into upper part of intestine of

left; right caecum small, opening below left one on right side; testis spherical, ventral to gut, in base of cone-shaped projection.

Embryo in both types located on dorsal right side between M III and IV. The horn-like projection is absent in very young individuals (as this is present in young *H. virgula* from the stolon, perhaps this is incorrect).

This species has been reported only from Seto, Japan (Komai, 1932), and the present specimen is from 7°4'N, 140°4'W. Komai (1932) described both the solitary and aggregate forms (one and ca. 30 specimens, respectively), considering them *S. (C.) virgula*. Ihle and Ihle-Landenberg (1936) studied *H. virgula* critically, comparing their observations with those of Komai. They concluded that his specimens were a distinct species which they named after him. Tokioka (1937) agreed with this conclusion and figured and described the gut and associated structures of gregarious specimens, apparently from the same collection on which Komai worked.

Fedele (1937) found that the dorsal tentacle above the ciliated groove of gregarious individuals is also present in *H. virgula*. He considered the spherical testis of *H. komaii* to be only a condition of age and therefore regarded Komai's specimens as identical with *H. virgula*. Ihle and Ihle-Landenberg (1938b) wrote a short note defending their earlier conclusion. They agreed that the dorsal tentacle is also found in *H. virgula*, but the spherical testis was not present; this conclusion is supported in the present report, as all stolonical individuals of *H. virgula* possess an elongate testis, never a spherical one. In addition, the solitary form of *H. komaii* is so different from *H. virgula* that they regarded their earlier conclusion as the correct one, with which I am in complete agreement.

SALPINAE subfam. nov.

This subfamily may be distinguished by the following characteristics: (1) In both forms the gut is completely free from the gill, except at the esophageal region, and does

not accompany the gill; (2) there are no distinct light organs present in either form (the gut of some species produces light from diffuse bodies); (3) the gut in the aggregate form is a more or less compact "nucleus," never a loosely formed loop or an extended tube; (4) attachment organs in the aggregate form are separated, not united into one process; thus, there are two or more attachment organs in each animal.

Genus *BROOKSIA* Metcalf, 1918

Solitary form with six body muscles, aggregate form with four and five. Solitary form with an anterior snout containing two pairs of longitudinal muscles, the dorsal pair continuous with the mouth musculature, the ventral pair formed by M I and C?. Ventral longitudinal muscles extend posteriorly to gut region. Aggregate form with testis outside intestinal coil, with short anteriorly upturned endostyle. Aggregate form asymmetric.

One species, *Brooksia rostrata*.

Brooksia rostrata (Traustedt) 1893

Fig. 9a-e

Salpa rostrata Traustedt, 1893: 8; Sigl, 1912b (fide Thompson, 1948).

Salpa (Brooksia) rostrata Metcalf, 1918: 50; Sewell, 1926: 84.

Brooksia rostrata Ihle, 1935: 527-529; Ihle and Ihle-Landenberg, 1935: 24; Thompson, 1948: 120.

SOLITARY FORM: More than 10 specimens examined, with length range of 2-31 mm. without snout (probable range of 4-62 mm. with snout). (Fig. 9b-e). *Test:* Flabby, glutinous, without permanent elevations or depressions; usually absent or fragmentary in preserved specimens. *Muscles:* Six dorsally continuous body muscles present; M I-III and IV-V-VI-x forming groups dorsally; M III-IV touching laterally; a strong longitudinal muscle coursing on each side of endostyle from gut to anterior tip of snout (they remain separate throughout their length);

these longitudinal muscles joined by M C? and M I only (this is contrary to Traustedt, 1893, and Thompson, 1948, but on close examination, one can see that no other muscle fuses with them as Ihle, 1910, showed). In addition to extensions of the ventral longitudinal muscles, the snout contains two dorsal longitudinal muscles that continue with the oral retractor. I have thus classified them as M b₃, or ventral lip sphincter 3. The oral retractor is formed by the first dorsal lip sphincter (A₁) and all three ventral lip sphincters. M B₁ and C extend to just behind the oral retractor. An independent muscle, probably formed from M C or B₁ (I have labeled it C?), extends ventrally to join the ventral longitudinal muscle, as does M I. In one specimen, M I is dorsally interrupted, probably unnaturally. The horizontal muscle (c) is long and relatively narrow. The cloacal musculature of Figure 9c, d has been reconstructed from fragments. *Ciliated groove, ganglion and eye:* Ciliated groove long, sinuous in large specimens, short and simple in smaller ones. The eye has the usual horseshoe shape. Ganglion and eye lateral to ciliated groove in large specimens, dorsal to it in smaller ones. *Viscera:* Gut somewhat compressed laterally; margined by a thin flap of caecum (?) tissue; in state E (Ihle and Ihle-Landenberg, 1935). The stolon is directed posteriorly.

AGGREGATE FORM: More than 10 specimens examined with length range of 0.8-2.5 mm. (Fig. 9a). *Test:* Flabby, glutinous, usually absent in preserved animals. *Muscles:* Body muscles fused dorsally and ventrally into a single mass; asymmetric, with two types produced, the sinistral and dextral individual, whose muscles are mirror images. There are apparently four body muscles on one side and five on the other, but due to the invariably poor condition of preserved specimens, musculature is difficult to study; consequently, this needs further examination. *Ciliated groove:* Simple, anterior to M I. *Viscera:* Anterior end of endostyle widely turned dorsally; endostyle short; gut in state A (Ihle, 1937-39);

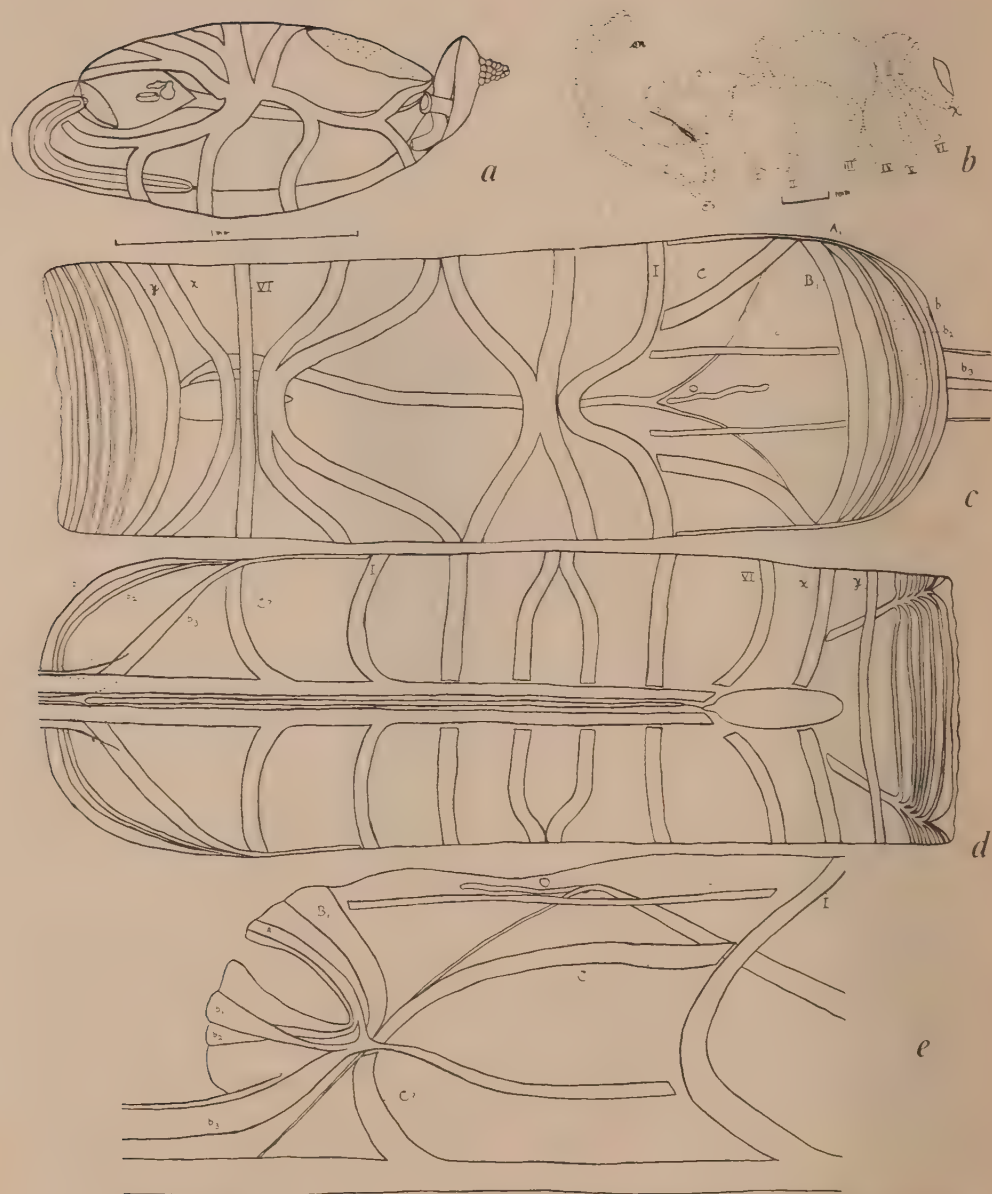


FIG. 9. *Brooksia rostrata*. a, Aggregate form, left dorsal aspect; b, solitary form, specimen without test, left dorsal aspect; c, solitary form, diagram of dorsal surface (length without snout, 31 mm.); d, same specimen as c, ventral surface; e, same specimen as c, mouth region, left lateral aspect.

testis located posterior to gut, unlike all other Salpinae.

This form, because of its small size, is easily confused with *Thalia democratica* agg. The presence of the widely turned endostyle, prominent gut with posterior testis, and dorsal and ventral muscle masses make it readily distinguishable.

Previously this species has been considered rare, although, as Apstein (1894) and Thompson (1948) stated, the very small aggregate form may easily be overlooked, especially among large numbers of *Thalia democratica* agg. The species is common in the POFI collections; in one plankton sample, for example, there were 8 solitary and 38 aggregate zooids. These animals are delicate and usually fragmented. Only two specimens of the solitary form retained the snout. The solitary zooid can be positively identified by the longitudinal muscles coursing parallel to the endostyle; the aggregate zooids must be examined closely, preferably stained, for correct identification. Fragments should not be overlooked but stained and examined, as the snout is useful as a recognition character only if the animal is whole. The high muscular activity of the solitary zooid was shown by the fact that in many specimens the body was turned completely inside out.

Genus *IHLEA* Metcalf, 1919

Solitary form with six or seven body muscles which form complete rings. Aggregate form with five or six body muscles which form complete rings or are ventrally interrupted; these muscles are arranged asymmetrically.

Two species, *Ihlea punctata* (type) and *I. magalhanica*. The latter species has not been found in the POFI collections.

Ihlea punctata (Forskål) 1775

Fig. 10a-c

Salpa punctata Forskål, 1775: 114; Ihle, 1912: 34.

Biphora punctata Bruguière, 1789: 181.

Salpa musculosa [?] Herdman, 1888: 64.

Salpa musculosa-punctata Traustedt, 1893: 6.

Salpa asymmetrica Fowler, 1896: 994; Ihle, 1912: 35.

Salpa (Salpa) punctata Streiff, 1908: 25.

Salpa (Apsteinia) punctata Metcalf, 1918: 72 (see also Metcalf, 1919).

Salpa (Apsteinia) asymmetrica Metcalf, 1918: 78, 183 (see also Metcalf, 1919).

Ihlea punctata Ihle, 1935: 527-529.

Ihlea asymmetrica Ihle, 1935: 527-529; Tokioka, 1937: 222; Berrill, 1950: 300.

SOLITARY FORM: Eight specimens examined, with length range of 3 (embryo)-14 mm. (Fig. 10a). **Test:** No specimen of the solitary and aggregate generations except the embryo had the test attached. It is probably loosely attached to the adult. The test of the embryo is flabby, rather thick around gut and elaeoblast area; without distinct elevations or de-

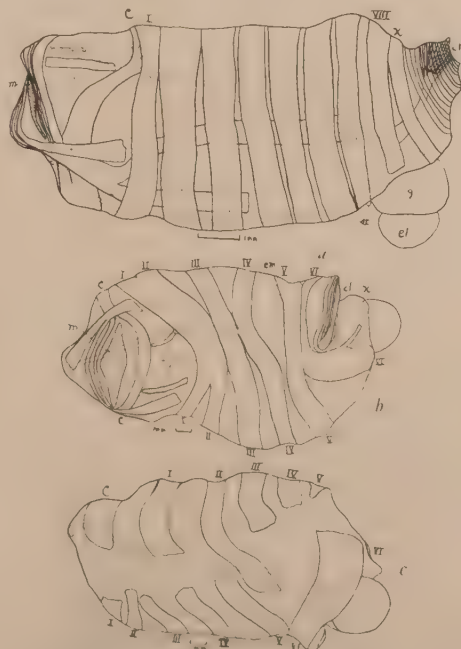


FIG. 10. *Ihlea punctata*. a, Solitary form, left side, slightly dorsal; b, aggregate form, dorsal aspect; c, aggregate form, ventral aspect.

pressions; with one lateral attachment organ on each side over cloacal muscle x. *Muscles*: Ten large muscles of which the first is M C; M I fused with C dorsally; M VI-VII fused ventrally; remaining body muscles distinct dorsally and ventrally; M C, I-VII, and x forming complete rings; M VIII interrupted ventrally, continuous dorsally; ventral oral retractor extending posteriorly on each side, branching into two longitudinal bands, a dorsal one extending to posterior edge of M VII and a ventral one extending to space between M III and IV (touching IV in embryo); longitudinal muscles coursing internally to body muscles; cloacal retractor extending anteriorly beneath x to M VIII. *Ciliated groove, ganglion and eye*: Ciliated groove simple, anterior to M C. Ganglion and eye just beneath M C. *Viscera*: Gut compact, in condition D (Ihle and Ihle-Landenberg, 1933); stolon, according to earlier investigators, forming a tight spiral limited to ventral region of gut (no stolon present in POFI specimens).

AGGREGATE FORM: More than 10 specimens examined with length range of 18-23 mm. (Fig. 10b,c). *Test*: Not observed but body flabby, thus test probably without permanent elevations or depressions. *Muscles*: Asymmetric; six body muscles present; M I-II join dorsally as do III-IV and V-VI; all muscles interrupted ventrally; M C broad; M VI on one side extending in broad band around ventral surface of gut; M II on side opposite latter portion of VI extending posteriorly on ventral surface toward opposite side to between M V and VI. *Ciliated groove, ganglion and eye*: All anterior to M I; ciliated groove straight, simple; ganglion and eye posterodorsal to it; eye projecting dorsally toward a small opening in mantle above it. *Viscera*: Gut compact, in condition F (Ihle and Ihle-Landenberg, 1933); embryo located on right side just under M V.

On examination of the literature of *Iblea punctata* and *I. asymmetrica*, a large number of contradictions, seemingly incorrect observations, and similarities in the descriptions of

the two so-called species are noticeable.

Therefore, if some of the earlier works which seem to be permeated with faulty observations are disregarded, the reported differences between the species and my criticisms of them may be summarized as follows:

1. In *Iblea asymmetrica* aggregate there are no pigment cells ventrally on the test, whereas in *I. punctata* these are present. The presence or absence of pigment is probably largely determined by length of exposure to the preservation fluid.

2. In *I. asymmetrica* agg. all body muscles are interrupted ventrally (Ihle, 1912; Tokioka, 1937) or only M VI is a ring (Metcalf, 1918), whereas in *I. punctata* all muscles are interrupted ventrally (Streiff, 1908; Ihle, 1912; Metcalf, 1918). Metcalf (1918) performed his study on stolon individuals of *I. asymmetrica* which perhaps had not completed their growth and thus possessed a ring muscle; or he made an error in his observation.

3. In *I. asymmetrica* agg., M I-II and V-VI join dorsally to form groups, M III and IV remain separate (Metcalf, 1918), or M I-II, III-IV, and V-VI form groups, the second group (III-IV) joining the first (Ihle, 1912; Tokioka, 1937). On the other hand, *I. punctata* forms two groups—M I-II and V-VI—and M III-IV remain separate (Streiff, 1908; Metcalf, 1918), or M I-II and V-VI form groups, M II-III remain separate but approach M II (Traustedt, 1893; Apstein, 1906a). These differences in muscle grouping seem to be only individual variation. They overlap in part and are considered nonuseful here.

4. In *Iblea asymmetrica* sol., the dorsal longitudinal muscle extends to M VIII; the ventral longitudinal muscle extends to beneath M V (Ihle, 1912; Metcalf, 1918). In *I. punctata*, on the other hand, the dorsal longitudinal muscle extends to between M VII and VIII (Apstein, 1906a; Streiff, 1908; Ihle, 1912; Metcalf, 1918); the ventral longitudinal muscle extends to between M III-IV (Apstein, 1906a; Streiff, 1908; Ihle, 1912; Metcalf, 1918). There is obviously no difference

in the dorsal longitudinal muscle extension. The difference described in the ventral extension is perhaps only one of growth. At any rate, it is rather minor.

5. In *Ihleia asymmetrica* sol. there are lateral projections on either side of the gut in embryos (and the small specimen of Ihle, 1912), whereas these have not been reported in *I. punctata* (Apstein, 1901, Ihle, 1912, and Metcalf, 1918, have reported them in *I. asymmetrica*). As Metcalf (1918) pointed out on his embryo, lateral projections are probably only embryonic attachment organs. Thus they may disappear in adults. They are presumably present in embryos of both so-called species.

6. In *I. punctata* sol. there are pigmented areas on the lips and posteroventral region near the gut (Metcalf, 1918), whereas these have not been reported in *I. asymmetrica*. Again, the presence or absence of pigment is probably largely determined by the length of exposure to preservation fluid.

7. In *I. asymmetrica* sol., the bow muscle (C) and I, II, III, and IV form one group dorsally, M VII, VIII, and x form another (Metcalf, 1918); or C-I-II form one group, III-IV form another, and M VIII and x form a third group (Apstein, 1901); or C-I-II form one group dorsally, M III-IV a second, and M VII-VIII-x form a third group (Ihle, 1912). On the other hand, in *I. punctata* C-I-II form the only group (Traustedt, 1893); or all remain separate (Apstein, 1906a,b; Streiff, 1908); or C-I-II form one group, and VII (?)—VIII-x (figures of Metcalf, 1918) form another. These differences in muscle grouping are probably only individual variation and are considered nonuseful here.

As a result of an exhaustive review of the literature, I can conclude only three possibilities: (1) the two species may be distinct, but, if so, the descriptions are in such a tangle that they are in large part unreliable; (2) the two so-called species are one, the differences described being due only to individual variation, not to specific, subspecific, varietal, or

formal variation; (3) the two species are one, the differences described being due to variations important enough, perhaps, to consider *I. asymmetrica* to be only a form or variety of the main species, *I. punctata*. This form would be distinguished from the main species only by the length of the ventral longitudinal muscle and the absence of pigmented areas in the test.

It is my opinion that possibility 2, above, is the correct one. Therefore, the two species are here regarded as only one, *Ihleia punctata* (= *I. asymmetrica*), with no differences other than what can be attributed to individual variation.

This conclusion is upheld by an embryo (solitary form) in the POFI collections. This embryo's ventral longitudinal muscle extends up to the anterior edge of M IV (a character of *I. punctata*, presumably); it also, however, possesses attachment organs—one on each side over M x (a character of *I. asymmetrica*, presumably).

Genus SALPA Forskål, 1775

Solitary form with eight ventrally interrupted body muscles, aggregate form with six. In the aggregate form, these muscles form two groups dorsally. Transverse ridges of gill bar taper gradually to a point ventrally and are separated from one another by a distance less than 0.5 the width of the gill bar.

Two species, *Salpa maxima* (type) and *S. fusiformis*.

Salpa fusiformis Cuvier, 1804

Fig. 11a-b, 12a-e, 15b, 16b

Salpa fusiformis Cuvier, 1804: 382; Bomford, 1913: 243; Ihle, 1935: 527-529; Tokioka, 1937: 223; Thompson, 1948: 156; Berrill, 1950: 293.

Salpa aspera Chamisso, 1819: 14.

Salpa runcinata Chamisso, 1819: 16.

Biphora depressa Sars, 1829: 51.

Biphora tricuspidata Sars, 1829: 56.

Salpa clostra Deshayes, 1836-46: vol. 121, figs. 2-2a.

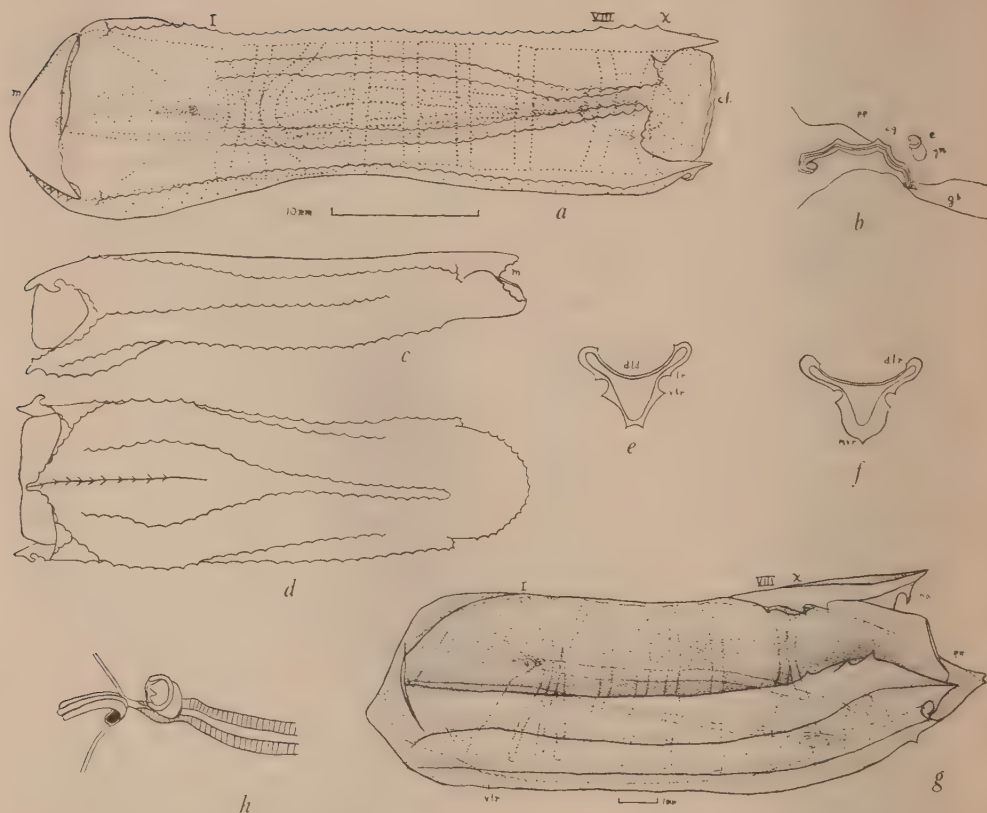


FIG. 11. *Salpa fusiformis*, solitary form. *a*, Asperate form, dorsal aspect; *b*, same specimen as *a*, ciliated groove and associated structures, dorsal aspect; *c*, same specimen as *a*, test, right side; *d*, same specimen as *a*, test, ventral surface; *e*, nonspiny form, scheme of cross section of test at level of M III; *f*, nonspiny form, scheme of cross section of test at gut level; *g*, nonspiny form, left dorsolateral aspect; *h*, same specimen as *g*, ciliated groove and associated structures, dorsal aspect.

Salpa runcinata-fusiformis Traustedt, 1885: 370.

Salpa echinata Herdman, 1888: 66.

Salpa runcinata-fusiformis var. *echinata* Apstein, 1894a: 47.

Salpa fusiformis var. *echinata* Apstein, 1894b: 14.

Salpa fusiformis-runcinata Ritter, 1905: 64.

Salpa fusiformis-runcinata form *echinata* Ritter, 1905: 67.

Salpa (Salpa) fusiformis Streiff, 1908: 24; Metcalf, 1918: 88; Sewell, 1926: 75; Stiasny, 1926: 424.

Salpa fusiformis forma *aspera* Ihle, 1911: 587; Tokioka, 1937: 223; Thompson, 1948: 158.

Salpa fusiformis fusiformis Ihle, 1912: 39.

Salpa fusiformis aspera Ihle, 1912: 40.

Salpa (Salpa) fusiformis form *aspera* Metcalf, 1918: 92; Sewell, 1926: 76.

SOLITARY FORM: More than 10 specimens examined with length range of 11–47 mm. (Fig. 11). *Test:* The typical form is described first (Fig. 11g): dorsal longitudinal depression wide and deep, limited on each side by a dorsal limiting ridge; each dorsal limiting ridge bearing posteriorly several spines, continuing into a dorsal posterior projection; test of dorsal longitudinal depression thin,

continuous with thin test of cloacal siphon; dorsal posterior projections bearing a blunt, straight, posterior spine and a curved ventral hook; each projection also forming a ventrally directed posterior ridge that joins the same ridge of opposite side midventrally; at joint, ventral posterior projection formed; each dorsal posterior projection bearing laterally an anteriorly directed lateral ridge; ventral to this, formed at the posterior ridge, a ventrolateral ridge courses anteriorly; ventrally a midventral ridge continuing anteriorly, dividing into two that continue to the chin; chin and mouth covered by thin test; internally test with rather large gut cavity, no elaeoblast cavity; cavity for posterior ventral attachment organ not present in typical specimens (may be present in large asperate specimens); margin of gut cavity smooth. The asperate form of this species is similar to the typical form, except that its ridges are spiny and the test has more thin area, being thick only posteriorly, at the chin and upper lip,

and along ridges (Fig. 11*a*). *Muscles*: Eight body muscles; M I-III and VIII-x usually fuse, touch, or converge but may be separated; no attachment organ between M VI-VII. *Ciliated groove*: Usually forming shallow open bend (Fig. 11*b*) but may form a large structure resembling that of *Salpa maxima* (Fig. 11*b*). *Viscera*: Gut compact, in condition E (Ihle and Ihle-Landenberg, 1933); endostyle straight; stolon usually coursing anteriorly, turning abruptly and coursing around left side of gut, but may form a tight circle around gut.

AGGREGATE FORM: More than 10 specimens examined with length range of 5-37 mm. (Fig. 12). *Test*: In typical form (Fig. 12*a*), keg-shaped, smooth; with one anterior and one posterior end projection; each may be as long as body; dorsal longitudinal depression extending onto end projections, limited laterally by dorsal limiting elevations; ventrally test gradually raised, forming a relatively small gut swelling. There is an asperate form (Fig.



FIG. 12. *Salpa furciformis*, aggregate form. *a*, Nonspiny form, dorsal aspect; *b*, asperate form, dorsal aspect; *c*, another asperate specimen, dorsal aspect; *d*, same specimen as *b*, dorsal aspect of ciliated groove and associated structures; *e*, ventral aspect of ciliated groove, from *d*.

12*b,c*) whose test is sparsely spined, asymmetric; end projections short, although Metcalf (1918) found some with long projections; test relatively thick. This form has broad muscle bands. *Muscles*: Six body muscles; M I-II and III-IV fusing dorsally as do M V-VI, thus forming two groups; M IV and V usually approach, touching or joining laterally, but as Stiasny (1926) pointed out, this is not so in many specimens; ends of muscles extending rather far ventrally. Ventral lip sphincter 4 (M *b*₃) interrupted. *Ciliated groove* (Fig. 12*d,e*): Simple, straight or slightly curved. *Viscera*: Gut compact, in condition C (Ihle and Ihle-Landenberg, 1933); gill segments closely approximated; embryo attached to right side dorsally behind or beneath M V.

Salpa maxima Forskål, 1775

Figs. 13*a-l*, 14*a-e*, 15*a*, 16*a*

Salpa maxima Forskål, 1775: 112; Ihle, 1935: 527-529; Tokioka, 1937: 223; Thompson, 1948: 154.

Salpa africana Forskål, 1775: 116.

Biphora maxima Bruguière, 1789: 179.

Biphora africana Bruguière, 1789: 182.

Salpa birostratus Blainville, 1827: 119.

Salpa chamissonis Lesson, 1830: 274.

Salpa forskalii [?] Lesson, 1830: 276.

Salpa birostrata Meyen, 1832: 412.

Salpa antarctica Meyen, 1832: 416.

Salpa naepolitana [?] Chiaje, 1841: 40.

Salpa africana-maxima Traustedt, 1885: 374.

Salpa (Salpa) maxima Streiff, 1908: 21; Metcalf, 1918: 83; Sewell, 1926: 83; Stiasny, 1926: 419.

SOLITARY FORM: Ten specimens examined with length range of 6 (embryo)-108 mm. (Fig. 13). *Test*: In typical specimen (Fig. 13*e*) thick in all areas, especially around gut; dorsal depression rather deep; two large dorsal limiting elevations; ventrolateral depression deep, gradually forming ventral elevation; spinose posteriorly; internally, test with large gut cavity whose posterior margin may bear elevations (called "baumförmigen Fortsätzen" of

the cloacal tube, and therefore presumably of epithelium, by Streiff, 1908, and Ihle, 1912, and figured as such by them as well as later investigators); these internal test elevations may be absent or present, usually bearing several blunt spines which themselves may bear minute spines; a cavity projects ventro-anteriorly from the gut cavity, housing the elaeoblast and reduced in older individuals that have resorbed the elaeoblast; anterior to gut cavity, a placental cavity present in smaller specimens; posterior to gut cavity a deep invagination for posteroventral attachment organ usually present; in one specimen (Fig. 13*e*), whole ventral region forming a cavity continuous with an opening in chin which appears to be natural, as its margin is not jagged, but not present in smaller specimens; chin prominent. In addition to the typical form, there is an echinate form that resembles the echinate form of *Salpa fusiformis* (Fig. 13*a*). It can be distinguished from the typical form only on the basis of the test. It should, perhaps, be described as typical, as this is the only form of the smaller specimens of *S. maxima* found here. Test has distinct thick and thin regions; thin dorsally and laterally except in posterior quarter of body; spines usually limited to posterior quarter of body (but not necessarily; see Fig. 13*l*); a deep longitudinal depression limited by dorsal limiting elevations (these may be ridges); transverse depression at base of upper lip; dorsal limiting elevations becoming thickened posteriorly, bearing a row of spines; just below this, a narrow longitudinal extension of thin test joins cloacal test; ventral to this a thickened region continuous posteriorly and ventrally from one side to opposite side; two weak ridges of spines on lateral surface of this thickened region; a group of spines on ventrolateral and ventral gut region; entire posteroventral region forming a gut swelling; ventral surface thickened along its entire length forming a large nonridged (but may be echinate) ventral elevation; chin rather prominent. The test as well as other structures

of *Salpa fusiformis* and *S. maxima* are in some specimens almost identical. Figure 13*l* shows a specimen of *S. maxima* of this type. **Muscles:** Eight body muscles, usually far separated from one another, but groups may be formed; extending only a short distance ventrally; attachment organ on each side dorsally between

M VI and VII that may be prominent, reduced, or absent (Fig. 13*b,f*). **Ciliated groove** (Fig. 13*g,h*): Forms a large incomplete loop with three bends; in larger specimens, minor bends give the appearance of segmentation. **Viscera:** Gut compact, in condition F (Ihle and Ihle-Landenberg, 1933); stolon extending

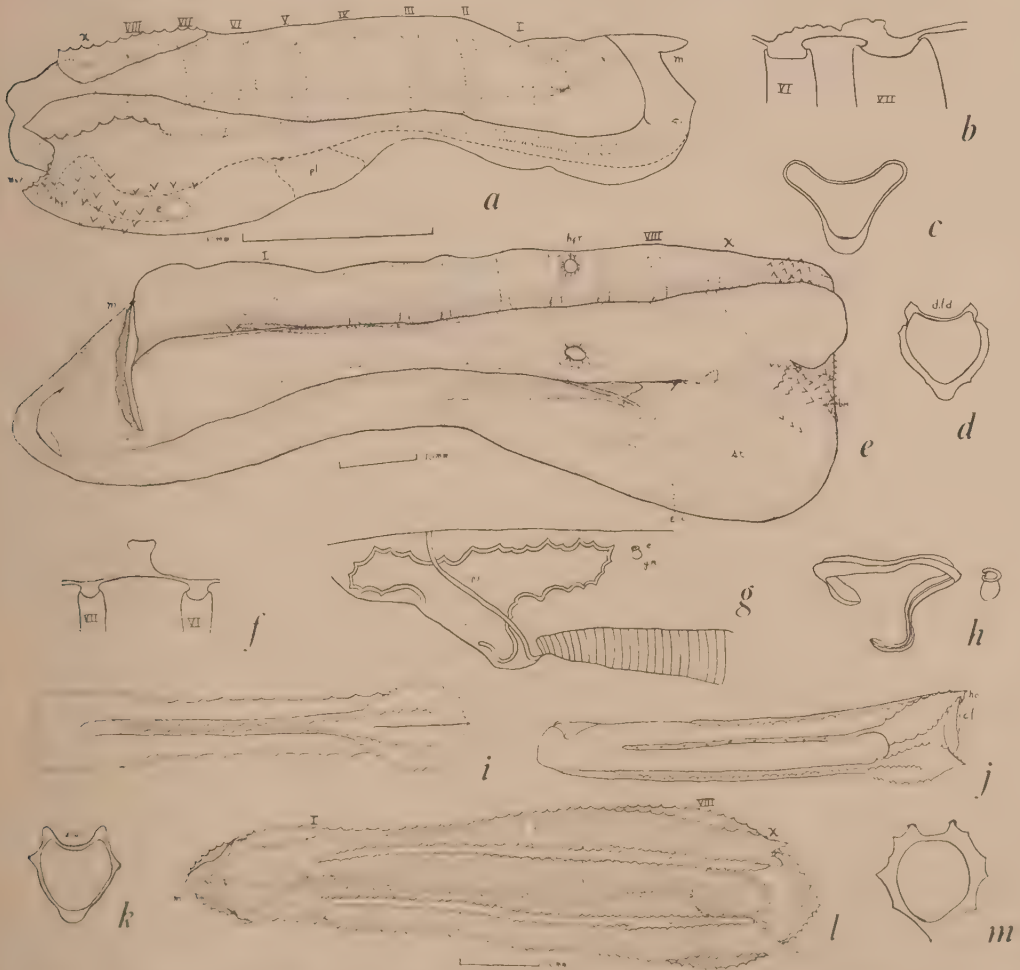


FIG. 13. *Salpa maxima*, solitary form. *a*, Smaller specimen, right side (the gut has been drawn up to reveal test cavities); *b*, dorsal attachment organ of a specimen similar to *a*, lateral aspect; *c*, same specimen as *a*, schematic cross section of test at level of M III; *d*, same specimen as *a*, schematic cross section of test at gut level; *e*, larger specimen, left side; *f*, same specimen as *e*, lateral aspect of dorsal attachment organ; *g*, same specimen as *e*, lateral aspect of ciliated groove and associated structures; *h*, same specimen as *a*, ciliated groove, ganglion and eye, dorsolateral aspect; *i*, echinate form, ventral aspect of test; *j*, same specimen as *i*, test from left; *k*, same specimen as *k*, schematic cross section of test at level of M III; *l*, another echinate specimen, dorsal aspect; *m*, same specimen as *l*, schematic cross section of test at gut level.

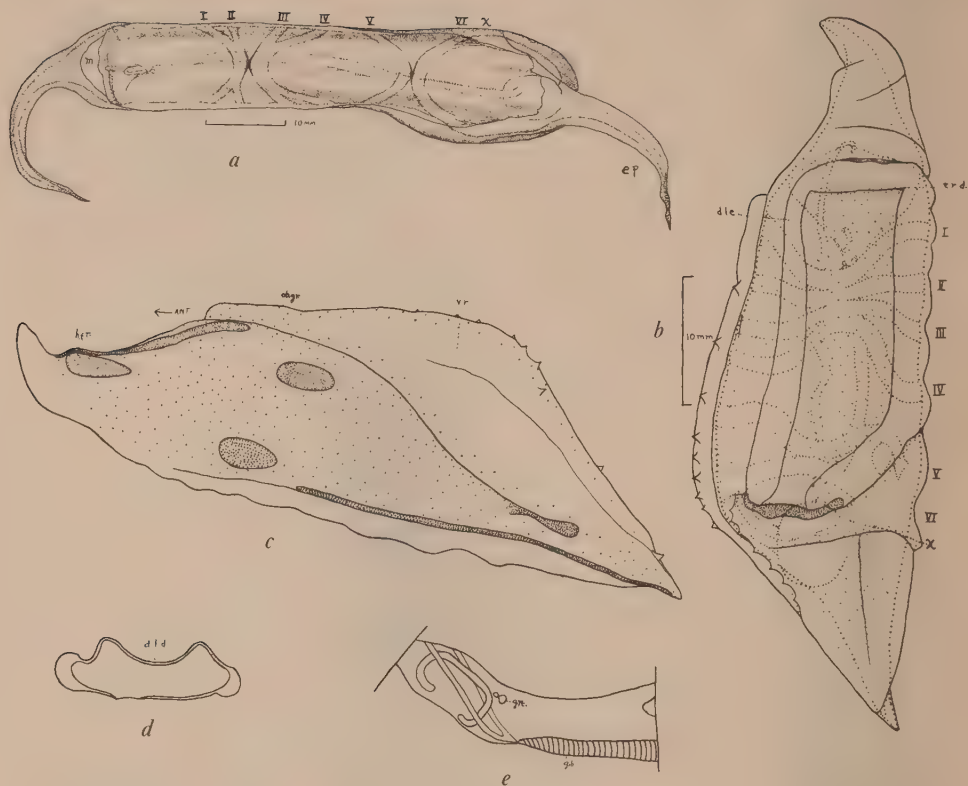


FIG. 14. *Salpa maxima*, aggregate form. *a*, Larger specimen, dorsal aspect; *b*, smaller (echinate) specimen, dorsal aspect; *c*, same specimen as *b*, ventral aspect of test; *d*, same specimen as *b*, schematic cross section of test at level of M IV; *e*, same specimen as *b*, left aspect of ciliated groove and associated structures.

anteriorly, turning posteriorly and usually rather closely encircling gut, then extending anteriorly again; a ventral posterior attachment organ usually present behind gut (Fig. 13*a, bft*).

AGGREGATE FORM: Over 10 specimens examined with length range of 10–112 mm. (Fig. 14). **Test:** In the typical (?) form, thick and smooth (Fig. 14*a*) in all areas; gut swelling prominent; end projections long or short; test bearing neither serrations, grooves, nor ridges; weak dorsal longitudinal depression and large ventral elevation present; gut cavity large, its margin smooth except for a V-shaped depression posteriorly. The most common form among POFI specimens is asymmetric, echinate, and smaller than the above-

described form (Fig. 14*b*). Test thick in all areas; dorsal longitudinal depression limited by dorsal limiting elevations; transverse depression at base of upper lip; posteriorly a sparsely serrated dorsolateral ridge with a sparsely serrated lateral ridge ventral to it; a dorsal transverse groove posterior to cloacal aperture with a longitudinal groove extending from it posteriorly on the end projection; few spines on or near gut swelling; nonserrated ventral ridge on gut swelling; oblique groove in front of gut swelling; remaining anterior test thin, forming a shallow depression; attachment organs prominent, large; end projections broad, relatively short. **Muscles:** Six present, forming two groups, M I–IV and V–VI; IV and V may approach laterally and

even touch; muscles extending far toward ventral surface. Ventral lip sphincter 4 (M_{b3}) continuous. *Ciliated groove* (Fig. 14e): Anterior to M_I , usually forming a large incomplete circle. *Viscera*: Gut compact, in condition C (Ihle and Ihle-Landenberg, 1933); embryo on right side dorsally between M_V and M_{VI} .

The form *tuberculata* of Metcalf has not been found in the collections studied.

Individuals of the species of *Salpa* (solitary form) smaller than 2 centimeters have characteristic features. The two species can be distinguished by the presence in *S. maxima* of a large elaeoblast and cavity, a large ciliated groove with three bends, the usually separated muscles, and the absence of a ventral hook on the dorsal posterior test projection, whereas *S. fusiformis* has opposite characteristics (except for the presence of an elaeoblast in very young animals). When the animals are larger, these distinctions become gradually less apparent; the elaeoblast becomes reduced or resorbed, although in all specimens of *S. maxima* its test cavity remains; the ciliated groove of large *S. fusiformis* (47 mm. maximum length of POFI specimens) may have the same structure as that of *S. maxima*; the body muscles may either be grouped or distinct in both species; the internal "baumförmigen Fortsätzen" may be absent in *S. maxima*; large individuals of *S. maxima* may develop a ventral hook on the dorsal posterior test projection exactly as in *S. fusiformis* (Fig. 13j). Attachment organs, test, ganglion and eye, stolon, gut, and endostyle are either the same in both species or intergrade between them. The only structure that I have found never to intergrade is the cavity in which the elaeoblast lies in *S. maxima*. In all specimens examined, the elaeoblast cavity, although reduced in larger individuals, was present when the animal was considered, by other means, to be *S. maxima*. In all specimens considered to be *S. fusiformis*, even those as small as 11 millimeters, neither the elaeoblast nor its cavity was present. In small *S. fusiformis* the

ciliated groove is a simple open one; in *S. maxima*, even in advanced embryos, the ciliated groove is large and possesses the characteristic three bends. Thus, the most important differences between the two species are (1) the presence in *S. maxima* of an elaeoblast cavity (both large and small individuals), and (2) the structure of the ciliated groove.

As a result of insufficient descriptions, it is impossible to determine from the literature whether the asperate forms described and fig-

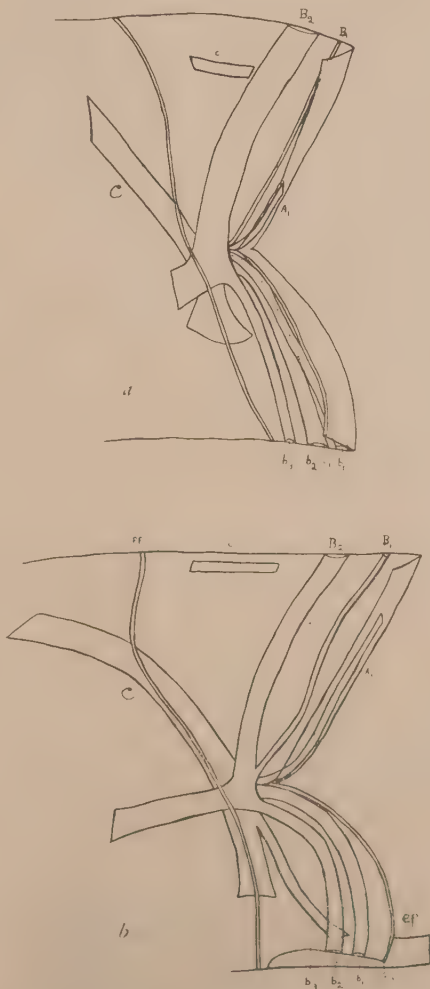


FIG. 15. Mouth musculature of left side, seen from inside. *a*, *Salpa maxima* agg.; *b*, *Salpa fusiformis* agg.

ured are *S. fusiformis* or *S. maxima* (see especially Herdman, 1888; Apstein, 1894b; Ritter, 1905; Ihle, 1910), although these were all considered *S. fusiformis*. I am inclined to regard the very large specimens described by some of these authors as *S. maxima*, but this is only speculation.

There is less difficulty in distinguishing the two species in the aggregate generation than in the solitary generation. Body muscle arrangement is a poor means of distinction (Stiasny, 1926). Nevertheless, it has been the main basis for differentiating *S. fusiformis* from other species. In the POFI collections, some individuals of *S. maxima* were found in which M IV and V touch laterally (usually considered a character of *S. fusiformis*), and many specimens of *S. fusiformis* were found in which, on either one or both sides, M IV and V do not touch. Other body structures, such as test, gut, position of embryo, and ciliated groove, are similar or intergrade between them. The differences in mouth musculature are the only certain means of distinguishing the two species in all specimens examined. In *S. maxima*, ventral lip sphincter 4 (M b₃) is continuous, whereas in *S. fusiformis* it is interrupted; there are also other differences as shown in Figure 15.

The great difference in size is usually a useful means of distinction between the species for both solitary and aggregate specimens.

Genus *WEEILIA* gen. nov.

The genus is characterized as follows: In both generations, transverse ribs of the gill bar meet dorsally, becoming reduced in width sharply toward the ventral surface so that they are far separated from one another ventrally (Fig. 16); gut in state E of Ihle and Ihle-Landenberg (1933) in both generations; aggregate form with five body muscles that form two groups dorsally (M I-III, IV-V); body muscles interrupted ventrally in both forms; no independent muscle in the posterior projection of the aggregate form; solitary form with eight (rarely nine) body muscles of which

M I-IV are either fused, joined by muscle strands, touch, or approach one another dorsally; body muscles may be split into branches laterally, sometimes are fused laterally, thus tending to vary considerably; no attachment organs in the solitary form (excluding lips and cloacal siphon); test of the solitary form (in POFI specimens) bears a varying number of thickened white patches that are arranged in rows; or, according to Brooks (1893), Sewell (1926), and Stiasny (1926), there are seven longitudinal ridges on the test—two dorsal, two lateral, and three ventral, with a posterior ridge joining the midventral ridge.

I regard *Salpa cylindrica* as sufficiently different from the other species of *Salpa* to be placed in a new genus, *Weelia*, named to honor Dr. P. B. van Weel of the University of Hawaii, who has contributed so significantly to the present study. The only known species, *Weelia cylindrica*, is the type.

Weelia cylindrica (Cuvier) 1804

Figs. 16c, 17a-f

Salpa cylindrica Cuvier, 1804: 381; Bomford,

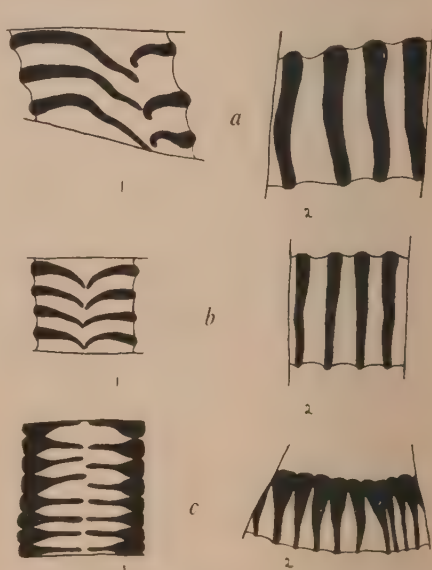


FIG. 16. Diagrams of a part of the gill bar of the solitary form. a, *Salpa maxima*; b, *Salpa fusiformis*; c, *Weelia cylindrica*. 1, ventral aspect; 2, lateral aspect.

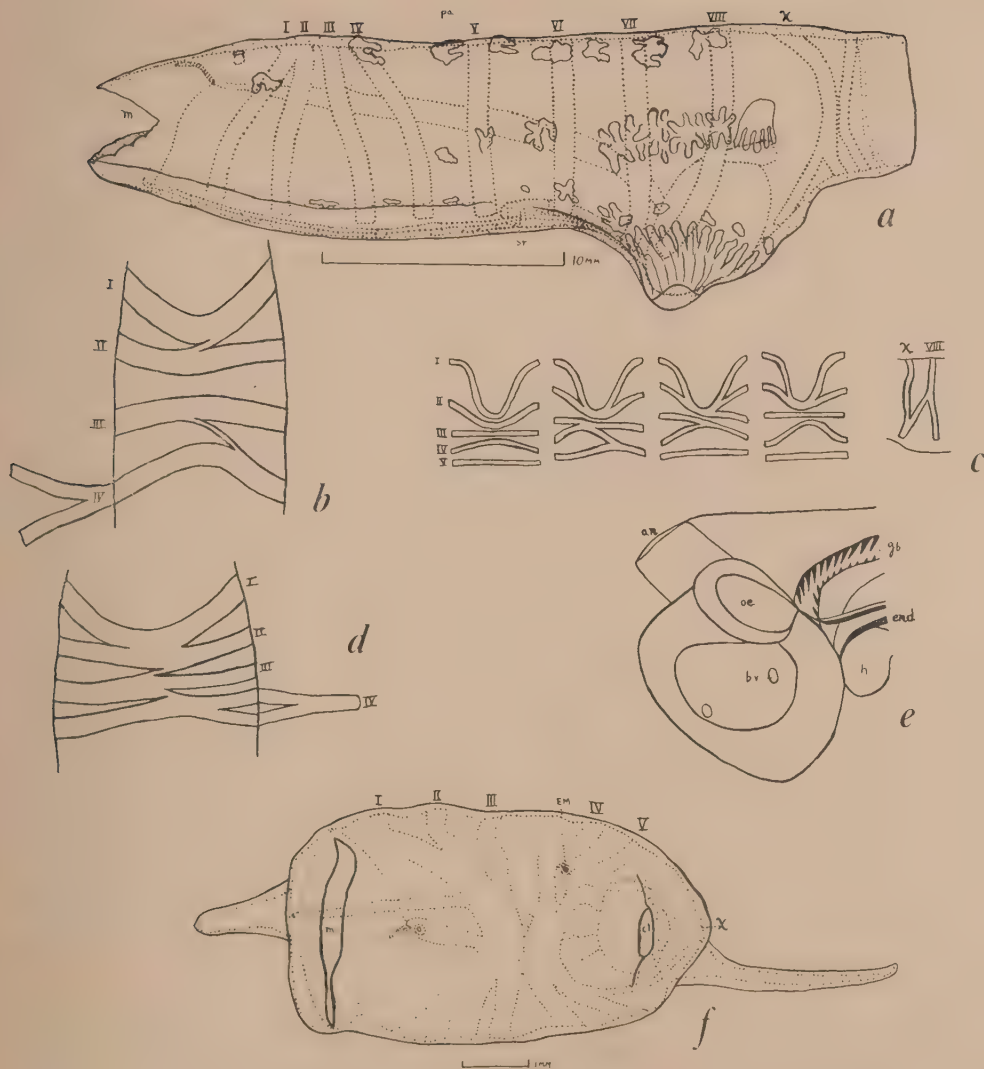


FIG. 17. *Weelia cylindrica*. *a*, Solitary form, left side; *b, c, d*, diagrams of muscle variation in the solitary form; in *b* and *d*, M IV is represented as being drawn out on one side (*c* after Sewell, 1926); *e*, gut of solitary form, right side; *f*, aggregate form, dorsal aspect.

1913: 243; Oka, 1915: 31; Ihle, 1935: 527
529; Tokioka, 1937: 223; Thompson, 1948:
161.

Weelia cylindrica Savigny, 1816: 235.

Salpa coerulescens Chamisso, 1819: 22.

Salpa elongata Blainville, 1827: 113.

Salpa garnotti [?] Lesson, 1830: 271.

Salpa truncata [?] Quoy and Gaimard, 1834:
588.

Salpa coerulea Quoy and Gaimard, 1834: 589.

Salpa (Salpa) cylindrica Metcalf, 1918: 93;

Sewell, 1926: 77; Stiasny, 1926: 429.

SOLITARY FORM: Over 10 specimens exam-
ined with a length range of 14–38 mm. (Fig.

17a). *Test*: Glutinous, dorsally and laterally thin, ventrally thickened especially over the gut as gut swelling; from anterior point of gut swelling, two weak ridges lacking spines coursing shortly anteriorly and posteriorly on ventral surface of gut swelling; anteriorly a sparsely spined ridge encircling base of ventral lip; chin weakly developed; attachment organs absent; a varying number of white patches of thickened test most prominent posteriorly, especially over the gut, arranged in three rows on each side: (1) a dorsolateral row, (2) a lateral row, and (3) a ventrolateral row at edge of thickened ventral test continuing with patches over gut. *Muscles*: Eight (sometimes nine, as described by Sewell, 1926) body muscles, some of which may divide into two branches laterally; M I-IV approaching, fusing, or joining by means of fine strands of muscle dorsally, varying considerably (Fig. 17b-d'); remainder of muscles usually equally separate from one another except x, which may approach M VIII dorsally; all body muscles extend rather far ventrally; some may be fused, but usually are separate. *Ciliated groove*: Simple, elongate, straight or slightly bent. *Viscera*: Gut compact, in condition E of Ihle and Ihle-Landenberg (1933) (Fig. 17e); stolon club-shaped, straight (or undulating according to Thompson, 1948); transverse ribs of gill touching one another dorsolaterally; tapering sharply and becoming rather far separated ventrally. In species of *Salpa*, these ribs are separate along their entire length and taper gradually toward the ventral surface (Fig. 16).

AGGREGATE FORM: Over 10 specimens examined, with length range of 6-16 mm. (Fig. 17f). *Test*: Flabby, without permanent ridges or grooves; one anterior and one posterior asymmetric projection, which are usually short and stumpy, but may be elongate as in Fig. 17f. Eight attachment organs present according to Stiasny (1926), but only six were visible in POFI specimens. *Muscles*: Five body muscles; M I-III fused dorsally as are M IV and V; in all POFI specimens the two groups are

joined dorsally (but may be distinct, according to other investigators); muscles extending rather far ventrally. *Ciliated groove*: Slightly arched, simple. *Viscera*: Gut compact, in condition E of Ihle and Ihle-Landenberg (1933); embryo on right side between M IV and V; gill as in solitary form.

This salp has been studied by many investigators, but only Brooks (1893) and, especially, Sewell (1926) have shown any of the great variation in muscle arrangement that occurs in the solitary form. The usual descriptions point out only that M I-IV approach or touch dorsally, the rest remain separate. The actual muscular arrangement may differ considerably from this condition (Fig. 17b-d'). In regard to the test of the solitary form, Brooks (1893), Sewell (1926), and Stiasny (1926) described seven longitudinal ridges—two dorsal, two lateral, and three ventral—as well as a posterior ridge. In all specimens I have examined, however, there are only two longitudinal ventral ridges present, and they are much shorter than those described by the above-named investigators. Evidently, there is also a rather large amount of variation in test structure. Almost all specimens, both aggregate and solitary, in the POFI collections are separated from their tests. In only a few individuals did the tests remain on the animals. I was unable to find the ridges described by Stiasny (1926) on the test of the aggregate form.

Genus RITTERIELLA Metcalf, 1919

Solitary form with 10 to 24 body muscles, all of which are ventrally interrupted, except in *R. amboinensis* the first three or four form complete rings. Aggregate form with six body muscles that form groups dorsally. Transverse ridges of gill bar are separated from one another by a distance greater than 0.5 the width of the gill bar. Solitary form possesses a blood-forming organ.

Two species, *Ritteriella amboinensis* (type) and *R. picteti*.

R. picteti and *R. amboinensis* were first de-

scribed by Apstein (1904) from Amboina. In 1906, Ritter described what he regarded as a new species, *Cyclosalpa retracta* (= *R. retracta*). This, however, was regarded by Ihle (1910) as similar enough to *R. picteti* to be a doubtful species if an intermediate form were found. Komai (1932) described such an intermediate form, so that at present *R. retracta* is considered a synonym of *R. picteti*.

***Ritteriella amboinensis* (Apstein) 1904**

Fig. 18a-c

Salpa amboinensis Apstein 1904: 651; 1906b (agg.): 166; Ihle, 1910: 34; 1912: 44.

Salpa (*Ritteria*) *amboinensis* Metcalf, 1918: 56; Sewell, 1926: 85.

Ritteriella amboinensis Ihle, 1935: 527-529; Tokioka, 1937: 222; Thompson, 1948: 126.

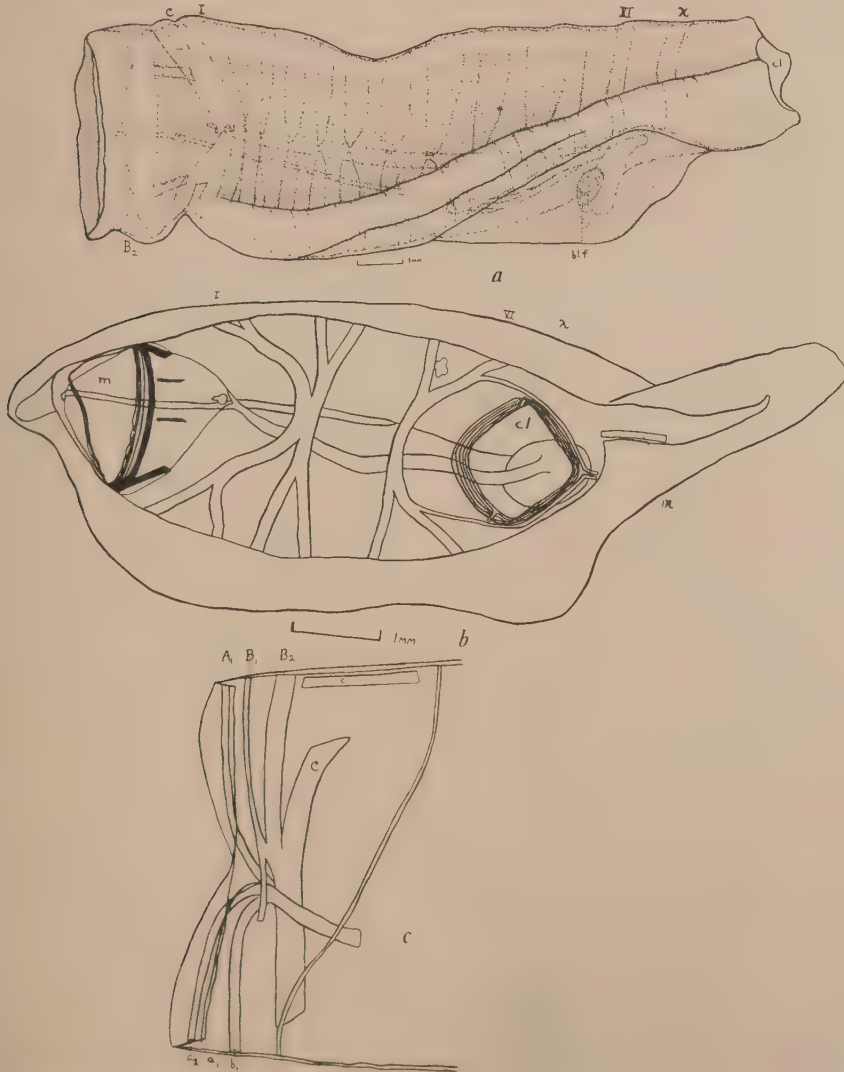


FIG. 18. *Ritteriella amboinensis*. a, Solitary form, dorsolateral aspect; b, aggregate form, dorsal aspect; c, aggregate form, mouth musculature of right side from inside.

[non] *Salpa amboinensis* Apstein, 1906a: 250; 1906b (sol.): 166.

SOLITARY FORM: Over 10 specimens examined with length range of 3 (embryos)–29 mm. (Fig. 18a). *Test:* Flabby, thin, especially over muscles; a rather thick, elongate gut swelling; there may be an additional swelling immediately over gut; no other permanent elevations or depressions. *Muscles:* Number of body muscles varies from 10 to 13, usually 11 or 12; number of muscles may be different on opposite sides of the body; M I–III touching dorsally as do X–XI and x; third upper lip sphincter muscle (B_2) distinct, large, continuous dorsally and ventrally; bow muscle interrupted dorsally, continuous ventrally; M I–III or IV forming rings; remainder of body muscles interrupted ventrally, becoming more widely interrupted posteriorly; all body muscles except I, II, X, and XI are joined dorsally by connecting bands of muscle; muscles relatively opaque and rather iridescent in all specimens examined. *Ciliated groove:* Simple, forming a crescent similar to that of *S. fusiformis* sol. *Viscera:* Gut rather compact, in condition A (Ihle and Ihle-Landenberg, 1933); stolon segmented only far anterior to gut, turning posteriorly at region of M V; a round or bean-shaped blood-forming organ present on left side of gut.

AGGREGATE FORM: Six specimens examined with a length range of 6–10 mm. (with projections) (Fig. 18b,c). *Test:* Flabby, glutinous; thin over whole body, slightly thicker over gut forming a rounded bulge; a general swelling of test material in gut area; end projections asymmetric, posterior one long, club-shaped, anterior one short, blunt. *Muscles:* Six body muscles of which M I–II and III–IV join dorsally into a group as do M V–VI; M I–II widely fused dorsally; all extend far toward the endostyle ventrally; a large, rather prominent independent muscle (*in*) on the posterior end projection under gut swelling, on right or left side according to position of animal on the stolon; this muscle much long-

er and more prominent than in any species of *Salpa*; M A_1 continuous dorsally; three ventral lip sphincters present. *Ciliated groove:* Situated vertically or almost so, a simple open structure. *Viscera:* Gut compact, in state D of Ihle and Ihle-Landenberg (1933); ribs or segments of gill bar relatively far separated; embryo attached beneath M V on right dorsal body wall.

Ritteriella picteti (Apstein) 1904

Fig. 19a–f

Salpa picteti Apstein, 1904: 655; 1906a: 252; 1906b: 168; Ihle, 1910: 43; 1912: 46.

Cyclosalpa retracta Ritter, 1906: 1.

Salpa amboinensis Apstein 1906a: 250; 1906b: 166.

[non] *Salpa amboinensis* Apstein, 1904: 651.

Salpa retracta Ihle, 1910: 40; 1912: 45.

Salpa (*Ritteria*) *retracta* Metcalf, 1918: 53.

Salpa (*Ritteria*) *picteti* Metcalf, 1918: 55; Sewell, 1926: 86.

Salpa (*Ritteriella*) *picteti* Komai, 1932: 65.

Ritteriella picteti Ihle, 1935: 527–529; Tokioka, 1937: 222; Thompson, 1948: 124; Berner, 1954.

SOLITARY FORM: Over 10 specimens examined with length range of 21–86 mm. (Fig. 19a,b). *Test:* Moderately thick over whole body with a slight elevation over the gut region; flabby and glutinous; no permanent elevations and depressions except over gut (Figure 19a represents an unusual condition in which there is present one lateral depression on each side; usually there is a single dorsal depression and no lateral ones). *Muscles:* Number varying from 13 to 24, including x and y, in the POFI specimens; number of muscles on one side usually different from number on opposite side; all body muscles continuous dorsally, interrupted ventrally; M I–V or VI usually connected by bands of muscle, remainder may be connected or distinct. *Ciliated groove:* Elongate, sinuous, but simple. *Viscera:* Gut in condition G (Ihle and Ihle-Landenberg, 1933), T-shaped with esophagus and

caecum forming right and left parts, respectively, of head of **T**; intestine forming posterior shaft of **T**; elongate, cylindrical, blood-forming organ located on left side, projecting from region of caecum dorsally, then bending anteriorly (abnormally posteriorly as in the figured specimen); stolon forming a slight bend and turning posteriorly at region of **M VI–VIII**.

AGGREGATE FORM: Two specimens exam-

ined, with length range of 18–23 mm., without end projections (Fig. 19*c–f*). *Test*: Flabby, glutinous, without permanent elevations and depressions except gut swelling which forms a large protrusion almost wholly independent of the rest of the body; end projections asymmetric, filiform. *Muscles*: Body muscles closely similar to those of *R. amboinensis* except wider and composed of more fibers (Berner, 1954); three sphincters in dorsal lip, of which the

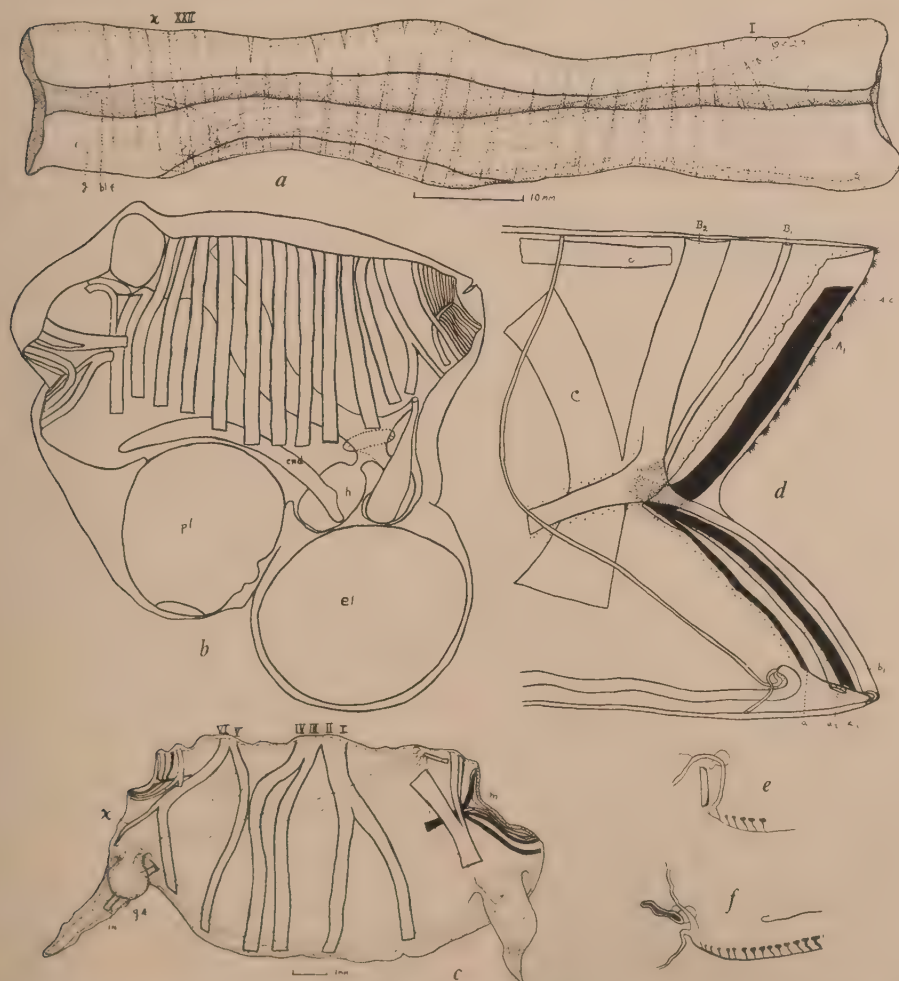


FIG. 19. *Ritterilla picteti*. *a*, Solitary form, right side; *b*, solitary form, left side of embryo (length, 1.3 mm.); *c*, aggregate form, right side; *d*, aggregate form, mouth musculature of left side from inside; *e*, aggregate form, ciliated groove, lateral aspect; *f*, aggregate form, ciliated groove, ventral aspect.

first is interrupted middorsally, the remainder continuous, and four continuous ventral lip sphincters; independent muscle large and conspicuous. *Ciliated groove*: Similar to that of *R. amboinensis* agg. *Viscera*: Similar to that of *R. amboinensis*, except that the endostyle extends almost to the gut in *R. picteti*, whereas it extends only to the level of M V or less in *R. amboinensis*.

The solitary forms of *R. picteti* and *R. amboinensis* are rather similar to one another. Descriptions of them, however, vary considerably and should be reviewed, as there is much overlapping between descriptions and probable errors in them. All descriptions agree in regard to gut structure (except for those of Apstein [1906*a*, 1906*b*] who evidently mistakenly identified his specimens as *S. amboinensis*). Ihle (1910) restudied these specimens and considered them to be *S. retracta*. They had the characteristic T-shaped gut structure of *R. picteti*.

In regard to muscle structure, however, there are a large number of contradictions. All past descriptions except Apstein's (1904) of *R. amboinensis* described M I-III as ring muscles. Apstein, however, in first describing the species, stated that the anterior muscles coursed almost to the endostyle and were thus interrupted. Ihle (1910) restudied these specimens that Apstein had described and stated for *R. amboinensis* sol. that "die 3 vorderen Körpermuskeln ebenso wie die Bogenmuskel ringförmig sind."

Sewell (1926), although not describing the condition, figured in *R. amboinensis* sol. M I-IV as ring muscles; in most POFI specimens here examined, M I-IV are ring muscles; in some specimens, only M I-III are rings.

Ritter (1906) emphasized the fact that in his specimen of *Cyclosalpa retracta* (= *R. picteti*), M 2-10 were completely continuous ventrally, thus ring muscles. This has not been observed in any other specimen of the species.

Apstein (1906*a*) described specimens, regarded by him as *S. amboinensis*, as possessing

four "vollkommene Rundmuskeln," although in his earlier description (1904) of *S. amboinensis* all body muscles were considered to be ventrally interrupted. Ihle (1910) restudied these specimens that Apstein (1906*a*) had studied and identified them as *S. retracta*. He stated that with this species all body muscles were ventrally interrupted. Later, however, Ihle (1912) described the species *S. retracta* as follows: "Vordere Muskeln ringförmig. . ."

In specimens of *R. picteti* described by Apstein (1904), Ihle (1910), Sewell (1926), Komai (1932), and Thompson (1948), all body muscles were described as ventrally interrupted. Apstein later (1906*a*, 1906*b*) made no mention of this condition even though he had done so in 1904. Ihle (1912), however, stated in regard to *R. picteti*, "Vordere Muskeln medio-ventral geschlossen." Also, Ihle (1935) characterized the genus *Ritteriella* as possessing 9-24 body muscles of which the "vorderen ringförmig sind."

Komai (1932) described a specimen of *R. picteti* in which all body muscles were ventrally interrupted. In regard to Ritter's (1906) description that *C. retracta* possessed nine ring muscles, Komai stated, "It is very doubtful whether one can put so much importance on that feature of the musculature in *R. retracta*, even if Ritter's observation on this point is warranted." I cannot agree with this statement, but rather believe that inconsistencies described have been the result of mistakes on the part of the observers. My conclusion is upheld by the POFI embryo, in which all body muscles and M C are ventrally interrupted.

The blood-forming organ of *R. amboinensis* has been described only as round or bean-shaped. In *R. picteti* (and *S. retracta*) it has usually been described as elongate, but Ihle (1910) described that of *S. picteti* as bean-shaped and that of *S. retracta* as variable in structure. Thus, this character perhaps is not important systematically.

Descriptions of the stolon also vary considerably. In *R. picteti* it varies from a spiral

(Apstein, 1906a, identified by him as *S. amboinensis*) to an elongate vermiform structure with a slight bend; in *R. amboinensis* it forms a wide sickle-shaped curve or is straight but may be slightly spiralled; thus, this organ also is perhaps not important systematically.

It is obvious from the literature that there has been a considerable amount of confusion in identifying the two solitary forms. Also obvious, both from the literature and POFI specimens, is the fact that these forms have a wide range of variability, perhaps more than any other salp, especially in muscle number and condition. I believe, however, that the differences in gut structure and in interruptions of the body muscles are important and valid differences. They are applicable to all POFI specimens, at any rate, except for the gut of the embryo of *R. picteti*.

The gregarious form of *R. amboinensis* has long been known (but that of *R. picteti* has only recently been described) by Berner (1954). Apstein (1904) first described the aggregate form of *R. amboinensis* rather inadequately, not describing the mouth or cloacal muscles. His figure does not permit accurate identification. Ihle (1910) studied this form next, describing both older chain forms and very young stolonial individuals. His descriptions are thorough and adequate for identification of *R. amboinensis* agg. He described and figured three sphincters in each lip (Taf. I, fig. 10) of the chain specimens. All these sphincters were described as uninterrupted. Metcalf (1918) based his description completely on that of Ihle (1910). He reproduced Ihle's figure 10 among others, thus showed *three* sphincters in each lip; but he described it as follows: "The oral muscles (Fig. 31) include a retractor and, in the upper and lower lips, two sphincters each. . . ." It may be thought that he considered the finer sphincters as only branches of one main sphincter, thus two in each lip, but in his other descriptions, each mouth muscle, no matter how small, was distinguished by a name and number. Therefore, he obviously

misread Ihle (1910) and, although reproducing Ihle's figure correctly, he described the animal incorrectly. Thompson (1948) based most of his descriptions on those of Metcalf (1918) and repeated Metcalf's error in the description of *R. amboinensis* agg. Thompson's figure shows only two sphincters in each lip, but as the figure is of the whole animal, details were probably overlooked in the mouth musculature. He also reproduced Ihle's figures (1910) but described the animal inaccurately, although Ihle had clearly labeled the three sphincters in each lip.

Berner (1954) identified the aggregate form of *R. picteti* by the embryo held within them and distinguished the form chiefly by the following features: (1) the body muscles are composed of more fibers and are thus wierd, and (2) the lip muscles of *R. picteti* include three sphincters in each lip, whereas there are only two in *R. amboinensis*. He apparently carried on the error of Metcalf and Thompson in his statement that the aggregate form of *R. amboinensis* has two sphincters in each lip.

I have found two specimens of the aggregate form of *R. picteti* in the POFI collections as well as six specimens of *R. amboinensis* and thus have been able to make a thorough comparison.

The major differences noted are:

1. *R. picteti* possesses three dorsal lip sphincters (A_1, B_1, B_2) and four ventral lip sphincters (a_1, a_2, a_3, b_1), one of which, a_2 , remains hidden beneath the more conspicuous a_3 ; in *R. amboinensis* there are three dorsal lip sphincters, one of which, B_1 , is very small and thus inconspicuous, and the ventral lip also contains three.

2. As Berner (1954) showed, in *R. picteti* upper-lip sphincter 1 (A_1) is interrupted mid-dorsally, whereas in *R. amboinensis* it is continuous.

3. The gut swelling of *R. picteti* is conspicuous and almost completely independent of the remainder of the body (as described in some specimens by Ihle, 1910; thus, if this

proves to be a useful difference, Ihle may have examined some specimens of *R. picteti* agg.), whereas in *R. amboinensis* it projects only slightly and is not independent of the remainder of the test.

4. The posterior end projection of *R. amboinensis* is large and club-shaped, whereas that of *R. picteti* is small and almost filiform.

5. The anterior end projection is short and blunt in *R. amboinensis*, whereas it is moderately long and filiform in *R. picteti*. Thus, if these last three differences are universal, these species deviate somewhat from the usual condition in salps in that the test is soft (but permanent structures are apparently present) and yet is useful in species distinction.

6. The endostyle extends further posteriorly in *R. picteti* than in *R. amboinensis*.

Both specimens of *R. picteti* contained embryos recognizable as this species, but the gut was not yet extended (Fig. 19*b*). No specimens of *R. amboinensis* contained embryos old enough to show structures nearing adult condition. The largest of these latter embryos (length, 0.3 mm.) contained nine recognizable body muscles, each of which,

however, was widely interrupted dorsally and ventrally. A study of a nearly mature embryo from an aggregate *R. amboinensis* is thus desirable.

Genus METCALFINA Ihle and Ihle-Landenberg, 1933

Solitary form with 10–13 asymmetric, ventrally interrupted body muscles; these are all joined dorsally. Aggregate form with six ventrally interrupted body muscles, of which M V and VI are independent from other body muscles. Test of both forms is firm and bears serrated ridges.

One species, *Metcalfina hexagona*.

Metcalfina hexagona (Quoy and Gaimard) 1824 Figs. 20*a–d*, 21*a–d*

Salpa hexagona Quoy and Gaimard, 1824: 505;
Bomford, 1913: 244; Oka, 1915: 30.

Salpa triangularis [?] Quoy and Gaimard,
1824: 511.

Salpa biensis [?] Blainville, 1827: 123.

Salpa lineata [?] Lesson, 1830: 268.

Salpa monotoma [?] Quoy and Gaimard, 1834:
591.

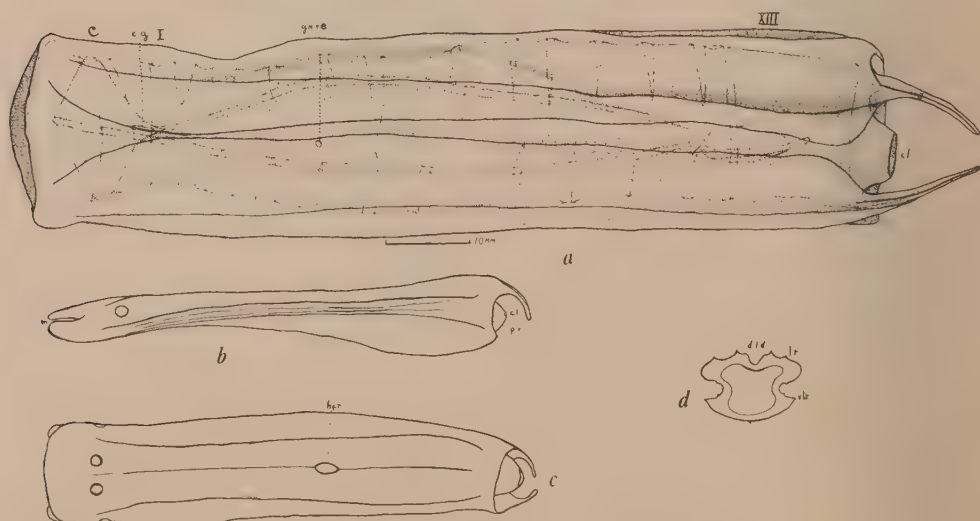


FIG. 20. *Metcalfina hexagona*, solitary form. *a*, Whole animal, dorsal aspect; *b*, test, left side; *c*, test, ventral surface; *d*, schematic cross section of test at level of ganglion.

Salpa (Jasis) hexagona Apstein, 1894a: 52.

Jasis hexagona Heider, 1895: 368.

Salpa (Ritteria) hexagona Metcalf, 1918: 62;
Sewell, 1926: 87.

Metcalfina hexagona Ihle and Ihle-Landenberg,
1933: 199; Ihle, 1935: 527–529; Thompson,
1948: 129.

SOLITARY FORM: More than 10 specimens examined with length range of 48–117 mm. with end projections (Fig. 20). *Test:* Traustedt (1885) figured the test accurately; unfortunately, his figures were not copied completely by Apstein (1906b), Metcalf (1918), and Thompson (1948), who left out the test ridges so well shown by Traustedt. The description of the test here agrees with that of Traustedt, but he did not figure or describe the attachment organs described here. Test firm; one posterior projection on each side that contains a mantle process which bears a sucker on its

tip. As Sewell (1926) pointed out, there are on each posterior projection five [minutely serrated] ridges. They are symmetrically located—one dorsal, two lateral, and two ventral. The lateral ridges of the projections are continuous with the posterior ridge of test encircling the cloacal siphon ventrally. There are 11 longitudinal ridges—four dorsal, six lateral, and one ventral (or four lateral and three ventral)—and one circular posterior ridge around the cloacal region ventrally, continuous with the posterior projections. In small specimens, all these ridges bear small or minute spines. In large specimens the spines are sparse and always minute. Chin and gut swelling moderately large. Attachment organs are relatively numerous on this solitary form; one disappears in the largest specimens. There are two anteroventral attachment organs at base of chin; a third, midventral and anterior to gut region, interrupts mid-

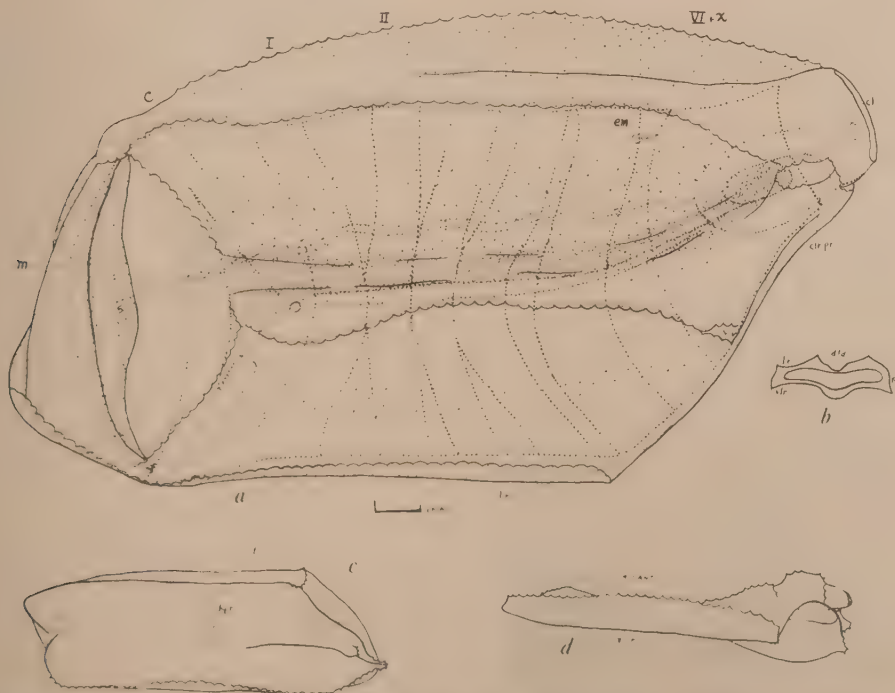


FIG. 21. *Metcalfina hexagona*, aggregate form. *a*, Whole animal, dorsal aspect; *b*, scheme of cross section of the test at M III level; *c*, test, ventral aspect; *d*, test, left side.

ventral ridge; it is absent in largest specimens; one lateral attachment organ on each side just behind angle of mouth. *Muscles*: Number varies, in POFI specimens ranging from 10 on one side and 11 on the opposite side to 12 and 13, respectively; muscles usually unequal in number on opposite sides; in POFI specimens, all body muscles irregularly continuous dorsally and connected dorsally by muscle strands except the last one, all interrupted rather widely ventrally (according to the figures of Traustedt, 1885, and Thompson, 1948, however, M I and II are distinct muscle bands); the last muscle much broader than other muscles; M C broad, continuous dorsally, widely interrupted ventrally. *Ciliated groove, ganglion and eye*: Ciliated groove elongate, straight, simple, located between M I and M C or under M C; ganglion and eye located far posteriorly, under M IV or V; eye a modified horseshoe (see Metcalf, 1918, fig. 39) with pigment at base and at each tip. *Viscera*: Gut moderately compact, in condition E (Ihle and Ihle-Landenberg, 1933); stolon forming a weak spiral, coursing anteriorly, bending and coursing posteriorly on left side of gut.

AGGREGATE FORM: More than 10 specimens examined with length range of 2 (stolon individual)—41 mm. (Fig. 21). *Test*: As with the solitary form, the aggregate form has been figured well by Traustedt (1885), Brooks (1893), and Apstein (1894b). Traustedt's figure, unfortunately, is of a dissected specimen, thus does not show the dorsal surface of the test. Test firm, asymmetric; middorsal depression thin, limited by weak grooves; dorsal limiting ridges on either side of depression, one always farther away from dorsal depression than other; these ridges continuing anteriorly into a circular ridge ringing the mouth widely; circular ridge on this side continuing posteriorly as lateral ridge ending after turning ventrally near level of gut; a prominent circular projection posteriorly over gut, flat on top and ridged; gut swelling and chin prominent; ventrolateral ridge not serrated

except on posterior tip (no equivalent ridge on opposite side of body); on opposite side a ventrolateral ridge (equivalent to lateral ridge above), serrated; in ventral view, a prominent midventral ridge over gut swelling disappearing anteriorly, forming a small posterior projection; all ridges mentioned except ventrolateral ridge on one side (left side in figures) and midventral ridge rather strongly serrated; thus six longitudinal ridges, one anterior circular one, and one posterior one below the cloacal siphon; attachment organs usually six—one large one at each end, one smaller circular one just anterior and posterior, respectively, to the latter, and two smaller circular ones midventrally. *Muscles*: Six body muscles, all interrupted ventrally, continuous dorsally; M I–IV forming a group dorsally, M V and VI independent; M V wider than first four, M VI much wider than V; M C broad, anterior part continuous middorsally; posterior part branching off from latter, interrupted dorsally. *Ciliated groove*: Moderately elongate, simple. *Viscera*: Gut compact, in condition E (Ihle and Ihle-Landenberg, 1933); endostyle sinuous; two to five, usually four embryos present.

Genus THETYS Tilesius, 1802

Solitary form with 16–22, aggregate form with 5, weakly developed body muscles which are widely interrupted ventrally. Some of them are also laterally interrupted. Test firm, with many large spines over surface but without serrated ridges.

One species, *Thetys vagina*.

Thetys vagina Tilesius, 1802

Figs. 22a–d, 23a–d

Dagysa notata [part.] Gmelin, 1791: 3131.

Thetys vagina Tilesius, 1802: 150; Ihle, 1935: 527–529; Tokioka, 1937: 224; Thompson, 1948: 136.

Salpa tilesii Cuvier, 1804: 375.

Dagysa strumosa Home, 1814: 71.

Salpa costata Quoy and Gaimard, 1824: 504.

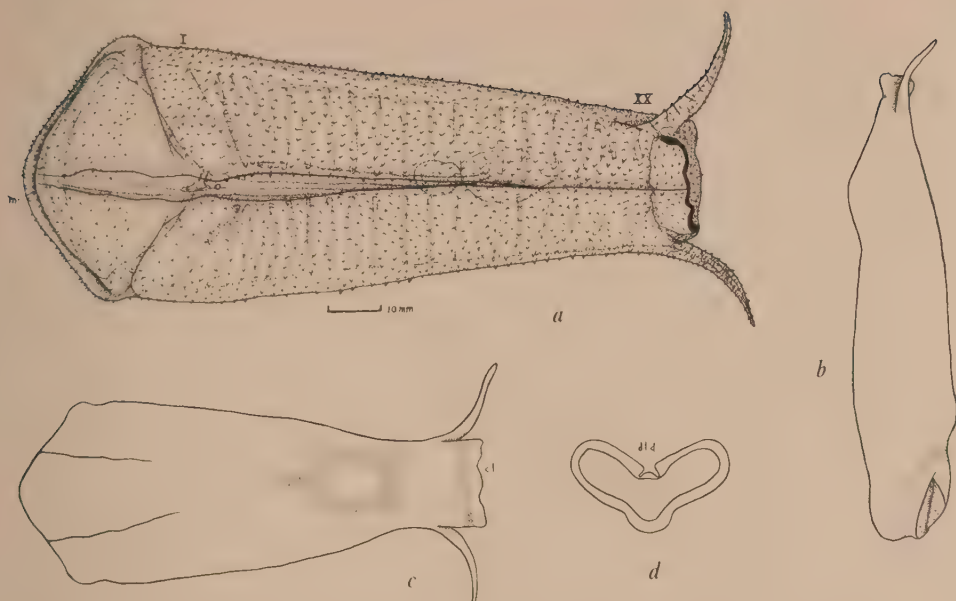


FIG. 22. *Thetys vagina*, solitary form. *a*, Whole animal, dorsal aspect; *b*, test, right side; *c*, test, ventral surface; *d*, schematic cross section of the test at gut level.

Salpa bigibbosa Quoy and Gaimard, 1824: 505.

Salpa gibbosa Quoy and Gaimard, 1824: 506.

Salpa infundibuliformis Quoy and Gaimard, 1824: 508.

Salpa costata-tilesii Traustedt, 1885: 379; Oka, 1915: 30.

Salpa sp. (?) n. sp. [?] Herdman, 1888: 62.

Jasis tilesii Lahille, 1890: 11.

Salpa (*Jasis*) *costata-tilesii* Apstein, 1894a: 50.

Salpa tilesii-costata Ritter, 1905: 70.

Salpa vagina Ihle, 1911: 587.

Salpa (*Thetys*) *vagina* Metcalf, 1918: 121; Sewell, 1926: 98; Stiasny, 1926: 446; Berrill, 1950: 299.

SOLITARY FORM: One specimen examined with length of 123 mm. without projections (Fig. 22). **Test:** Firm and thick except on inturned lips and on cloacal siphon; large spines occurring irregularly over whole surface; a prominent posterior projection on each side of cloacal siphon, containing tube of mantle epithelium with no sucker; dorsal depression limited by a groove on each side of a raised middle region, the whole limited by

broad limiting elevations; shallow lateral depression; midventral elevation raised over gut and chin as swellings; transverse groove at base of dorsal lip, continuing laterally to angle of mouth; one swelling on each side of dorsal surface posterior to transverse groove; base of ventral lip with a weak circular depression; transverse groove at base of cloacal siphon; one short, weak, longitudinal depression crossing each side of chin ventrally. **Muscles:** Twenty weakly developed muscles (number varies from 16 to 22 according to Thompson, 1948); all interrupted dorsally and ventrally, often elsewhere, accompanied by prominent blood vessels; muscles not extending to ventral surface, but blood vessels do; M I–IV or VI converge dorsally. **Ciliated groove:** Forming a large open loop. **Viscera:** Gut large, compact, in state E (Ihle and Ihle-Landenberg, 1933); located far anteriorly, at about the posterior third of body; endostyle broad, straight; stolon coursing anteriorly, bending and coursing posteriorly on left side of gut (Traustedt, 1885).

AGGREGATE FORM: Seven specimens examined with length range of 33–71 mm. (Fig. 23). *Test:* Asymmetric, thick and firm except on lips and cloacal siphon; dorsal depression broad, extending from dorsal lip to above cloacal siphon; a broad dorsal limiting elevation on each side; transverse groove at base of dorsal lip; other transverse grooves and folds occurring incidentally over test; lateral depression shallow or forming deep grooves; ventral surface greatly thickened, especially over chin and gut swelling; large spines with a rather constant arrangement over test according to animal's location on the stolon; three longitudinal rows on dorsolateral elevation of one side, one row extending posteroventrally onto gut swelling; gut swelling with few spines on posteroventral region; on opposite side of test, two longitudinal rows on dorsolateral elevation continuing anteroventrally with a group of spines crossing lateral depression, extending onto chin; several spines

present on posterodorsal and posteroventral regions of gut swelling; one group of spines extending transversely over dorsal lip; scattered spines in middorsal depression. Number of attachment organs varies, asymmetric in arrangement. *Muscles:* Five body muscles, interrupted dorsally and ventrally, extending only to sides of body; weakly developed, being interrupted in various places; M I–III converging dorsally but not touching; M V bifurcates; prominent blood vessels accompanying muscles. *Ciliated groove:* A large open loop. *Viscera:* Gut compact, in state E (Ihle and Ihle-Landenberg, 1933); endostyle narrow, sinuous; three or four embryos attached dorsally between M IV and V (Thompson, 1948).

Except for *Helicosalpa komaii* (230 mm.), the solitary form of this species is the largest of the salps (up to 226 mm. according to Traustedt, 1885). It was well figured (solitary form) by Traustedt (1885) and Stiasny (1926).

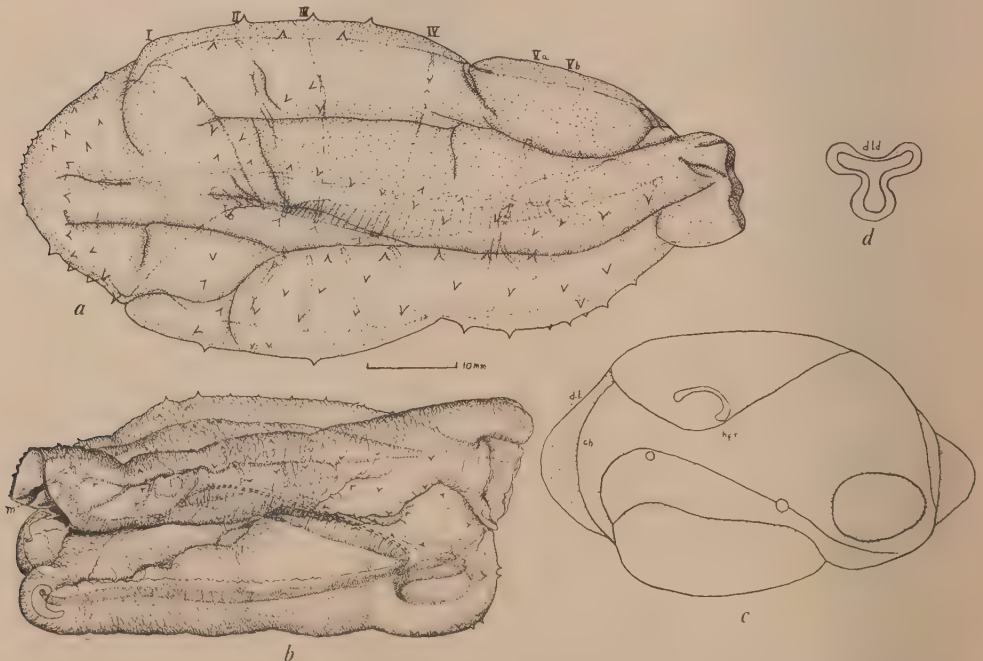


FIG. 23. *Thetys vagina*, aggregate form. *a*, Whole animal, dorsal aspect; *b*, another specimen, lateral aspect (length, 38 mm.); *c*, same specimen as *a*, ventral aspect of test; *d*, schematic cross section of test at level of M III.

The stolon individual (aggregate form) was well figured by Traustedt (1885) and Tokioka (1937). The preceding description (solitary form) agrees with their reports except for minor details.

Genus PEGEA Savigny, 1816

Four ventrally interrupted body muscles in both forms. Aggregate form with eight prominent, symmetrically arranged attachment organs.

One species, *Pegea confoederata*.

Pegea confoederata (Forskål) 1775

Figs. 24, 25

Salpa confoederata Forskål, 1775: 115; Bomford, 1913: 244.

Biphora confoederata Bruguière, 1789: 181.

Salpa gibba [?] Bosc, 1802: 178.

Salpa socia Bosc, 1802: 180.

Salpa scutigera Cuvier, 1804: 577.

Salpa octophora Cuvier, 1804: 577.

Salpa vivipara [?] Péron and Lesueur, 1807: pl. 31, fig. 3.

Pegea octofora Savigny, 1816: 235.

Salpa ferruginea Chamisso, 1819: 23.

Salpa informis Quoy and Gaimard, 1824 [*vide* Thompson, 1948].

Salpa bicaudata Quoy and Gaimard, 1827: 225.

Salpa laevis [?] Lesson, 1830: 273.

Salpa nephodea [?] Lesson, 1830: 275.

Salpa dolium [?] Quoy and Gaimard, 1834: 575.

Salpa femoralis [?] Quoy and Gaimard, 1834: 577.

Salpa scutigera-confoederata Traustedt, 1885: 362; Oka, 1915: 31.

Salpa quadrata Herdman, 1888: 84.

Pegea confoederata Lahille, 1890: 11; Ihle, 1935: 527-529; Tokioka, 1937: 230; Ihle and Ihle-Landenberg, 1938a: 107; Thompson, 1948: 143.

Salpa (Pegea) scutigera-confoederata Apstein, 1894a: 42.

Salpa (Pegea) scutigera-confoederata forma bicaudata Apstein, 1894a: 43.

Salpa confoederata-scutigera Ritter, 1905: 80.

Salpa (Salpa) confoederata Streiff, 1908: 32.

Salpa (Pegea) confederata Metcalf, 1918: 127; Berrill, 1950: 297.

Salpa (Pegea) confederata bicaudata Metcalf, 1918: 139.

Salpa (Pegea) confoederata Sewell, 1926: 100; Stiasny, 1926: 448.

SOLITARY FORM: More than 10 specimens examined with length range of 14-85 mm. (Fig. 24). *Test:* There are two different forms of this animal, the one characteristic of larger specimens, the other of smaller specimens. In the large form, test usually pear-shaped, smaller posteriorly, thick on ventral surface, especially over gut; dorsally a broad, slightly thickened elevation extending from upper lip to cloacal opening; this elevation limited laterally by one dorsolateral groove on each side; test very thin and flabby on lateral surface, therefore with no permanent shape; a prominent ventral elevation limited on each side by a ventrolateral groove; gut swelling prominent, produced as an additional swelling over the elaeoblast; test in all specimens examined not spiny, but earlier investigators have noted serrations on some specimens. In the small form, test pear-shaped, thick all over, firm, smaller posteriorly than anteriorly; on dorsal surface a shallow depression or deep groove extending from upper lip to cloacal opening; this depression limited by dorsal elevations; laterally a shallow depression extending from angle of mouth almost to region of gut; ventrally a rather strong elevation extending from lower lip almost to cloacal opening; this elevation further raised over elaeoblast as a disc-like bulge and bearing a far anterior small circular depression in which is located an attachment organ. The smaller form agrees more closely to the type set up by Stiasny (1926), but individuals are often different from his type. Thus, this animal deviates from the conclusion set up earlier here; that is, even though its test is firm and there may be grooves (but no ridges), these grooves probably are not permanent, and a definite "type"

cannot be established for it. Stiasny (1926) figured and described a longitudinal depression midventrally, limited to the anterior part of the test. I have not seen such a depression on any of my specimens, but in all the smaller ones there is a small circular depression for an attachment organ, which perhaps is what he saw. This is absent in larger specimens. The elaeoblast is relatively much larger in smaller specimens but is always a much-flattened disc. *Muscles*: Four body muscles; M I and II converging dorsally as do M III and IV; laterally all muscles diverging from one another, thus forming two X-shaped figures dorsally; muscles short. *Ciliated groove*: A large vertical loop whose ends approach one another anteriorly. *Viscera*: Gut compact, in state H (Ihle and Ihle-Landenberg, 1938a); elaeoblast forming a disc beneath gut; stolon encircling gut closely; endostyle weakly sinuous; on each side of endostyle at level of gut, a row of raised projections which have been noticed only by Ihle and Ihle-Landenberg (1938a), who described them as "Falten des Pharynxbodens" (*f* in Fig. 24). (These are not present in the aggregate generation.)

AGGREGATE FORM: More than 10 specimens examined with length range of 4–48 mm. (Fig. 25). *Test*: Loose, flabby, thin except around gut swelling and occasional thickened regions; gut swelling prominent, bearing

ridges or elevations above and below a circular longitudinal depression which is very shallow; ventral surface usually with a rather thickened narrow elevation; thin membranous sheets of test material may extend loosely out from gut swelling; in bicaudate specimens, two triangular extensions of test containing mantle epithelium extending dorsolaterally over gut swelling, one to each side of cloacal opening; on all specimens, two lateral and two ventral attachment organs on each side of body, making a total of eight; attachment organs tubular, prominent, symmetrical. Stiasny (1926) figured prominent ridges both ventrally and dorsally in addition to the gut ridges. My specimens do not agree with this; as the test is flabby, presence of depressions and elevations is considered here to be a matter of chance. The cloacal siphon forms a weak flap. *Muscles*: As in the solitary form, M I and II form an X-shaped group dorsally, as do M III and IV; they extend only to the lateral surface. *Ciliated groove*: Forming a large loop whose ends approach anteriorly. *Viscera*: Gut compact, in state C of Ihle and Ihle-Landenberg (1933); endostyle sinuous; embryo on right dorsal region between M III and IV.

The subspecies *bicaudata* of Metcalf (1918) is perhaps only a slight modification of the typical form. Sewell (1926) stated: "I

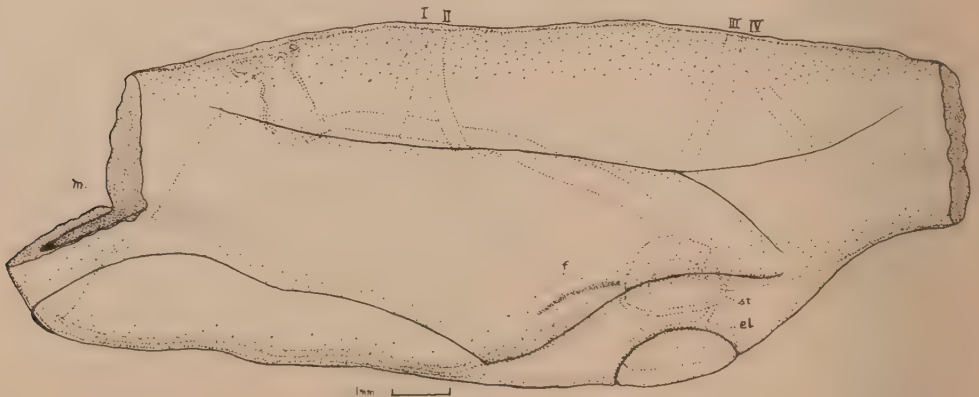


FIG. 24. *Pegea confederata*, solitary form, left side.



FIG. 25. *Pegea confederata*, aggregate form, left side.

can see no justification for considering the *bicaudata* form to be even a variety, and much less a distinct subspecies, as Metcalf has done." Although I have seen only a few (all very small) specimens of this form, and thus little intergradation, Sewell's reckoning is considered probably correct here, and the *bicaudata* individuals are not given subspecific status.

Genus *TRAUSTEDTIA* Metcalf, 1918

Solitary form with 7 to 25 tentacles, aggregate form with two or three. Solitary form with five, gregarious form with four, body muscles that are widely interrupted ventrally.

One species, *Traustedtia multitentaculata*.

Traustedtia multitentaculata

(Quoy and Gaimard) 1834

Figs. 26a-e, 27a-d

Salpa multitentaculata Quoy and Gaimard, 1834: 596; Bomford, 1913: 244.

Salpa bensenii Traustedt, 1893: 9.

Salpa verrucosa Apstein, 1894b: 12.

Salpa (Traustedtia) multitentaculata Metcalf, 1918: 147; Oka, 1921: 1; Sewell, 1926: 105.

Salpa (Traustedtia) multitentaculata bicristata Metcalf, 1918: 143.

Salpa (Traustedtia) radiata Metcalf, 1918: 152.

Salpa (Traustedtia) bensenii Oka, 1921: 10-14.

Traustedtia multitentaculata Ihle, 1935: 527-529; Tokioka, 1937: 230; 1938: 234; Thompson, 1948: 147.

SOLITARY FORM: Five specimens examined with length range of 2-16 mm. (without pro-

jections) (Fig. 26a). **Test:** Thick, especially on crests, gut swelling, chin, and lips; in dorsal view, a raised median depression extending posteriorly to form the cloacal flap, anteriorly to the greatly thickened transverse ridges of the upper lip; continuing anterolaterally with a vertical elevation that joins its fellow of the opposite side midventrally under the chin; dorsal depression limited by grooves or depressions on each side which form the bases of the prominent dorsal limiting ridges (crests); crest covered with peculiarly shaped spines (see Fig. 26c, also Apstein, 1894, Taf. II, fig. 13), continuing with one break posteroventrally below and behind cloacal opening, meeting fellow of opposite side there; cloacal flap bearing a small projection on each side; each crest bearing a moderately long tentacle directed posteriorly; a posteroventral unpaired tentacle, which is doubtless the remains of the elaeoblast attachment as suggested by Thompson, projecting posteriorly; 10 other paired tentacles on posterior lateral to ventral anterior surface, some of which may be quite long; thus, a total of 25 tentacles present in this specimen; chin and gut swelling prominent; ventral lip bearing several ordinary spines and a median row of peculiar flattened spines (Fig. 26d); dorsal lip with two high transverse ridges at base; internal surface of dorsal lip bearing a series of longitudinal and transverse grooves and ridges that are serrated; chin smooth or serrated. **Muscles:** Three main muscle masses—first including fused M I-III, second large M IV, and third, M V and x; all except V branching on each side; M IV and V joining ventral cloacal muscles; all muscles extending only a short distance laterally. For descriptions of mouth and cloacal muscles, see Metcalf (1918), Oka (1921), Sewell (1926), and Thompson (1948). **Ciliated groove:** Simple, straight, located directly under ganglion and eye. **Viscera:** Gut forming an elongate loop, in state D of Ihle and Ihle-Landenberg (1933) (Fig. 26e); stolon forming a loose circle around gut; endostyle extending anteriorly to base of ventral lip.



FIG. 26. *Traustedia multitentaculata*, solitary form. *a*, Whole animal, right side, slightly from the front; *b*, schematic cross section of the test between M III and IV; *c*, body spine, 48X; *d*, ventral lip spines, 24X; *e*, gut from right side.

AGGREGATE FORM: Six specimens examined with length range of 4–13 mm. without projections (Fig. 27). The figures of Trausted (1893), and especially Tokioka's descriptions and figures (1938), are excellent. The tentacles of this form are at most three, usually two. In addition, however, there are attachment organs that Sewell (1926) considered tentacles; this error was corrected by Thompson (1948). *Test:* Stiff, thick in all areas, especially

on chin and gut swelling; mantle often far separated from test dorsally; weak dorsal elevation extending from base of cloacal flap to base of dorsal lip, limited by transverse grooves at these places; cloacal flap very large; laterodorsally, a bulging limiting elevation on each side of dorsal elevation, continuous to chin and posteriorly forming tentacle; tentacles three in young specimens: two lateral posterior, and one median posterior projecting

from end of gut projection; larger specimens without midposterior tentacle; Sewell (1926) and Tokioka (1938) figure those of the small individuals as possessing transverse constrictions, as do small POFI specimens, but the constrictions are much sparser here; tentacles flat at base, filamentous distally, with one dorsal ridge, and one ventral ridge which is continuous with posterior ridge that fuses with its fellow of the opposite side over gut; in lateral view, a broad lateral depression or narrow groove, ventral to dorsal limiting elevation, extending from base of tentacle to chin, which is smooth in POFI specimens, contrary to Sewell (1926, fig. 40) and the statement of Thompson (1948: 152); a broad

ventral elevation extending from chin into gut swelling; posteriorly gut swelling forming a prominent projection bearing six large spines; four symmetrically arranged attachment organs on each side. The depressions and elevations of the test are variable. *Muscles*: Two main masses, of which the first consists of M I–II, the second of M III–IV and x; first muscle mass interrupted dorsally, second forming a distinct joint dorsally, as shown by Tokioka (1938); M IV does not help form ventral cloacal muscles, contrary to figures of Apstein (1904) and Thompson (1948); muscles extend only a short distance toward ventral surface. For a complete description of mouth and cloacal muscles, see Tokioka

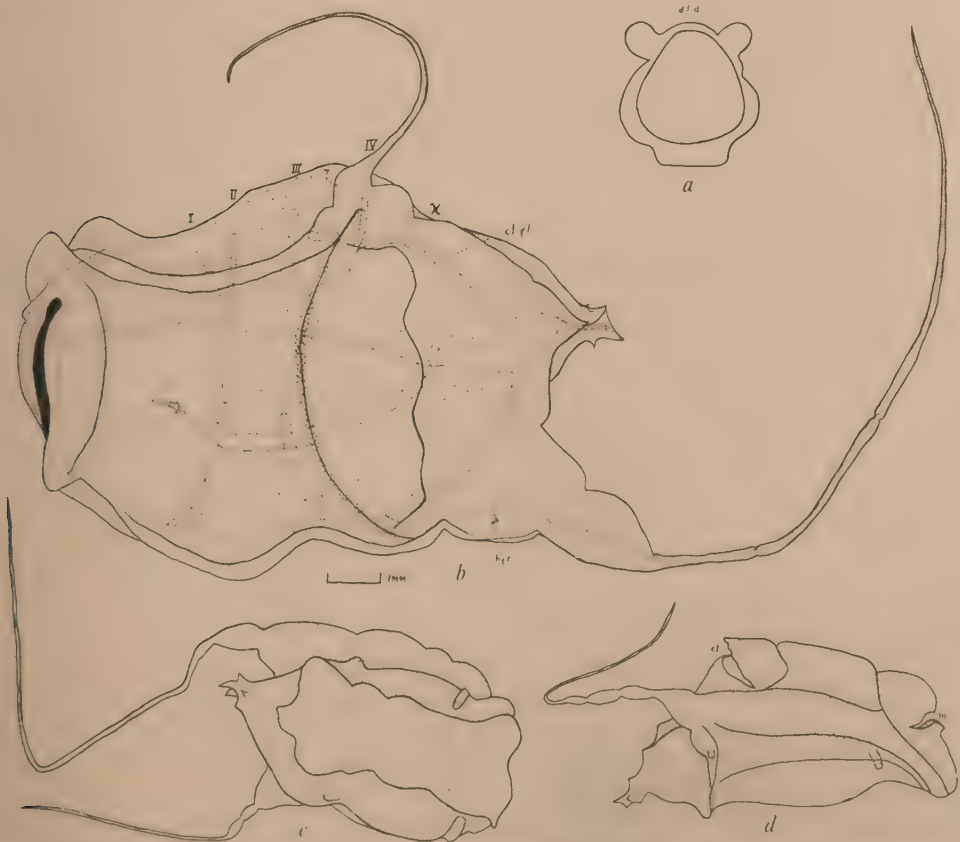


FIG. 27. *Tranostedia malintotacdata*, aggregate form. *a*, Schematic cross section of the test at level of M II; *b*, whole animal, dorsal aspect; *c*, test, ventral aspect; *d*, test, right side.

(1938). *Ciliated groove*: An open crescent; a broad languet below ciliated groove at junction with gill (Tokiooka, 1938, fig. 5). *Viscera*: Gut forming elongate loop in which course of intestine is obscured by large number of testis lobules; in condition D of Ihle and Ihle-Landenberg (Tokiooka, 1938); gut connected by long mantle projection with posterior gut projection; the mantle projection extending into median posterior tentacle, if present, as shown by Tokiooka (1938); endostyle weakly sinuous; embryos two, lateral to joint of M III-IV on right side.

All the solitary forms described by Metcalf (1918) are probably one species, as Sewell (1926) believed. Oka (1921), however, recognized two species, *Salpa (Traustedia) multitenaculata* and *S. (T.) henseni*, the latter being Metcalf's *S. (T.) radiata*, on the basis of the presence of eight tentacles in the former (according to my classification, 13, as he did not include in his count two paired and one unpaired pointed processes which are essentially similar to tentacles) and 20-23 in the latter. The conclusion that there is only one species is supported by the great variation in number of tentacles (varying from 7 to 25 in POFI specimens) and the probability that the radiate forms described by Apstein (1906a) and Dober (1912) simply were flattened dorso-ventrally, giving the impression of a radiate form; this probably also explains the horizontal position of the gut of these specimens, as Sewell (1926) remarked. Sewell stated that differences in details of musculature are often due to conditions of preservation, which perhaps is the cause of differences described by Metcalf (1918). Both Oka (1921) and Sewell (1926) considered Metcalf's subspecies *bicristata* to be invalid. In POFI specimens the crested condition is one of intergradation, but crests are always present, apparently due to age differences. In one small (2 mm.) individual the crests are very small; they become more pronounced in larger individuals.

The only basis for considering the various forms distinct, according to Oka (1921) and

Sewell (1926), is the different number of tentacles. Sewell (1926) distinguished between "true tentacles" and projections that penetrate the test but do not extend beyond the body margin. This, however, is probably only a condition of age and is not considered a useful distinction except for descriptive purposes. Oka (1921) remarked on the probable similarity of his "tentakeln" and "kurze . . . Anhänge" which projected from each side-wall of the cloacal opening. He also referred to "verborgene Tentakel" (those projecting into the crests and the unpaired posterior one). He did not describe any other projections. In the largest POFI specimen (Fig. 25a) all projections are of the true tentacle type, although many project only slightly beyond the test margin. In Sewell's (1926) and Thompson's (1948) specimens, there were nine tentacles present, including those not projecting beyond the body margin; in Apstein's (1894b) specimen there were eight, but, as Sewell (1926) remarked, there possibly were 13; in Metcalf's (1918) specimen and in Oka's (1921), 13 tentacles; and in Apstein's (1906a) and Dober's (1912) specimens, there were 20 and 23 tentacles present. Sewell (1926) thought there was a possibility that the differences were due to either geographic variation or variation in size. POFI specimens seem to confirm the latter conclusion as the number of tentacles is less with the smaller individuals and greater with larger ones. The smallest (2 mm.) specimen examined bore *no* "true tentacles" but bore seven mantle projections: one unpaired posterior; one pair of postero-lateral projections (the "posterior tentacles" of Sewell and Oka and tentacle 6 of Metcalf); one pair of projections in the cloacal siphon (5 of Metcalf); one pair in the posterior part of the crests (4 of Metcalf).

Further, in a specimen of 7 millimeters length, the projections are still not "true tentacles." This specimen is so poorly preserved, however, that I am unable to ascertain the number of projections present.

In another specimen, 11 millimeters long,

the same relationships exist as in the 2-millimeter specimen described above, except the posterolateral projections (6 of Metcalf) are true tentacles and of the same length as the body.

In the largest specimen examined (16 mm.) there are 25 tentacles, as described above.

Thus, it is my belief that the tentacles also do not show variations that would lead to the separation of any of Metcalf's forms from the main species. It would be desirable to re-examine some of the larger specimens (for example, Oka's specimen of 23 mm. length), described as possessing 13 or fewer tentacles, with the use of toluidin blue. If these large specimens actually possess only 13 or less tentacles, then *T. henseni* should probably be recognized also, as Oka (1921) has done.

All aggregate forms described to the present time have been regarded as only one species, *T. multitentaculata*, and all POFI specimens agree with this conclusion.

Genus *Thalia* Blumenbach, 1810

Solitary form with five body muscles of which the first four form rings; aggregate form with five ventrally interrupted body muscles, with a short endostyle. Languet present in both forms ventral to the ciliated groove.

Two species, *Thalia democratica* (type) and *T. longicauda*. The latter species has not been found in the collections studied.

Thalia democratica (Forskål) 1775

Figs. 28a-e, 29a-f

Salpa democratica Forskål, 1775: 113; Bomford, 1913: 244.

Salpa mucronata Forskål, 1775: 114.

Biphora democratica Bruguière, 1789: 180.

Biphora mucronata Bruguière, 1789: 181.

Salpa cyanogaster [?] Péron and Lesueur, 1807: fig. 3.

Thalia lingulata Blumenbach, 1810: (30).

Salpa spinosa Otto, 1823: 303.

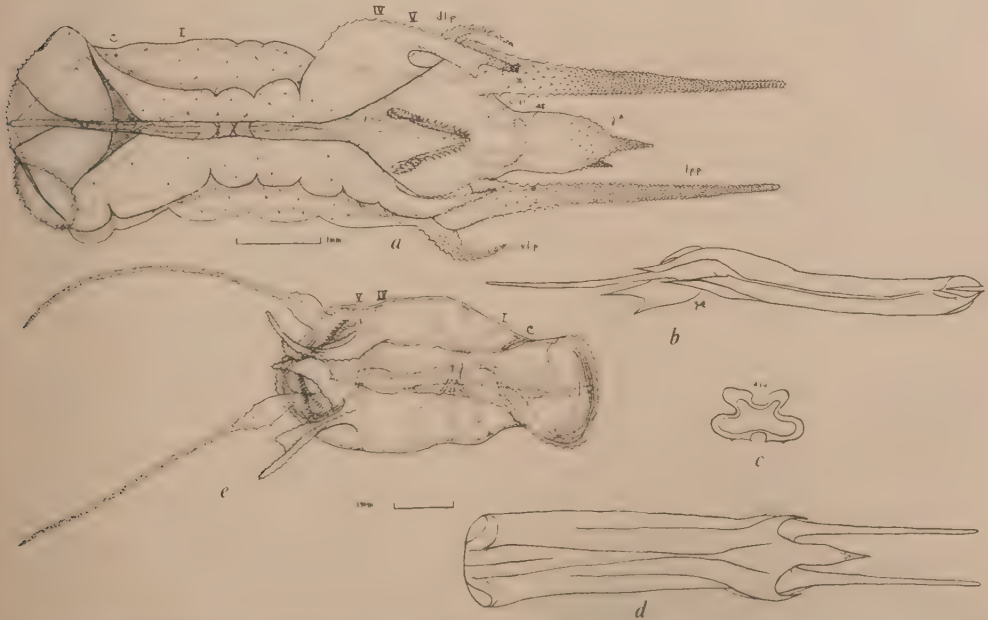


FIG. 28. *Thalia democratica*. solitary form. a, Echinate form, dorsal aspect; b, another specimen, test, right side; c, same specimen as b, schematic cross section of test at level of M III; d, same specimen, test, ventral surface; e, nonspiny form, dorsal aspect.

- Salpa rhomboides* [?] Quoy and Gaimard, 1824: 510.
Salpa rhomboidea [?] Blainville, 1827: 115.
Dubreuillia cirrhosa Lesson, 1830: 278.
Salpa pyramidalis [?] Quoy and Gaimard, 1834: 593.
Salpa caboti Desor, 1848: 75.
Salpa democratica-mucronata Traustedt, 1885: 365.
Thalia mucronata Lahille, 1890: 11.
Salpa (Thalia) democratica-mucronata Apstein, 1894a: 44.
Thalia democratica Heider, 1895: 368; Ihle, 1935: 527-529; Thompson, 1948: 139.
Salpa (Salpa) mucronata Streiff, 1908: 38.
Salpa (Thalia) democratica Metcalf, 1918: 109; Sewell, 1926: 92; Stiasny, 1926: 441; Ber-rill, 1950: 291.
Thalia democratica var. *orientalis* Tokioka, 1937: 226.
Thalia democratica var. *orientalis* forma *echinata* Tokioka, 1937: 229.

SOLITARY FORM: More than 10 specimens examined with length range of 4-9 mm., without projections (Fig. 28). *Test:* The echinate form (Fig. 28a) is discussed first. Test thick, especially over gut; gutswelling bearing two projections, one posterior and one ventroposterior; one usually long, lateral posterior projection on each side of body having no ridges but bearing many minute spines; one dorsolateral projection on either side of cloacal flap (atrial palp of Tokioka, 1937), ridged, bearing minute spines; each dorso-lateral projection bearing a truncate medial portion extending posteriorly; one ventro-lateral projection, usually smaller than the dorsolateral projection, extending posteriorly on each side of gut region; each a simple projection bearing minute spines; latter may be lacking, as Tokioka (1937) reported; thus, a total of six posterior projections of body and two of gut swelling; anteriorly, test truncate, ringed by an echinate ridge, with anteriorly projecting lip flaps; transverse dorsal groove at base of dorsal lip lying posterior to two bulges, one on each side of dorsal de-

pression; dorsal depression widening anteriorly and posteriorly, limited by dorsolateral limiting elevations that continue posteriorly into lateral ridges of dorsolateral projections; in posterior widening of dorsal depression, high triangular cloacal flap projecting posteriorly, bearing a dorsal echinated ridge on its margin, a ventral heavily fringed margin below; ventral lip of cloacal opening similarly fringed, margined by a deep transverse groove; a deep lateral depression (seldom, a groove) present; a ventrolateral elevation, continuous with ventrolateral projections, coursing anteriorly; ventral surface bearing a midventral depression limited by midventral limiting ridges originating at ventrolateral projections; a prominent short midventral ridge present beneath chin. The smooth form is much like the above, having the same projections on the posterior end (often the ventrolateral projections are absent as in Fig. 28e), same cloacal flap structure, and the anterior ridge around the mouth; dorsal depression and limiting ridges present (these may be only elevations). The test, however, is not spiniferous ventrally and is sparsely so dorsally; it is thin and flabby. The muscles of this form are narrower than those of the echinate form. *Muscles:* One large bow muscle (C) interrupted dorsally, continuous ventrally; five body muscles present; M I-IV continuous dorsally and ventrally; M V continuous dorsally, narrowly interrupted ventrally (Metcalf, 1918, says M V is continuous ventrally, but all other investigators described it as interrupted, as here); M I-III converge in midline dorsally as do M IV and V, thus forming two dorsal groups; M III and IV converge, usually touch midventrally. *Ciliated groove:* Far separated from ganglion and eye, bearing a languet projecting ventrally into the pharyngeal cavity. *Viscera:* Gut elongate and U-shaped, in state B (Ihle and Ihle-Landenberg, 1933); projecting far into gut swelling; endostyle extending only from level of M III forward; stolon forming a close circle or spiral around gut.

AGGREGATE FORM: More than 10 specimens examined with length range of 1–12 mm. (Fig. 29). **Test:** The echinate form (Fig. 29a) is discussed first. Test asymmetric, thick, stiff, with prominent, sparsely spiniferous ridges and with deep grooves and depressions; middorsal depression (limited to anterior region in some specimens) limited by spiniferous dorsal limiting ridges; depression constricted at base of dorsal lip, widening anteriorly around mouth; a transverse ridge in front of cloacal flap; cloacal flap hemispherical rather than triangular, fringed as in solitary form; gut swelling projecting in a point toward rear (this may be very long in young specimens as figured by Apstein, 1906a, Sewell, 1926, and Tokioka, 1937), bearing five spiniferous ridges that are usually symmetrically arranged; lateral ridges asymmetric, spiniferous; anterior end almost truncate; ventrally a single deep groove in a broad depression cut off anterolaterally by an oblique spiniferous ridge that connects with anterior end; gut swelling with a strong ventral ridge; attachment organs varying in number, elongate and filiform (but usually not projecting beyond test margin). There is a great amount of test variation as reported by Stiasny (1926). In the smooth form (Fig. 29e), test flabby, without spines of any kind, with long attachment organs usually projecting beyond test outline; no permanent ridges or grooves, but there may be depressions and elevations; protruding gut swelling; cloacal flap with fringes. **Muscles:** Five body muscles; M V relatively narrow; all muscles continuous dorsally, interrupted ventrally; M I–III in contact dorsally, forming a group as do IV and V. **Ciliated groove:** Far anterior; simple, with a languet projecting into pharynx. **Viscera:** Gut compact, in condition B (Ihle and Ihle-Landenberg, 1933); elongate; protruding far into gut swelling; endostyle short, extending anterior to level of M I or II only; embryo far behind M IV on right ventral body wall.

The variety *orientalis* recognized by Tokioka (1937) is based on the following differences:



FIG. 29. *Thalia democratica*, aggregate form. a, Echinate form, dorsal surface; b, same specimen, test, ventral surface; c, same specimen, test, right side; d, same specimen, schematic cross section of test at level of M III; e, smooth form, right side, slightly dorsal; f, scheme of cross section of test at gut swelling of specimen in a.

small size; atrial palp bifurcated; smooth appearance of the testis lobes. Moreover, he distinguished the form *echinata* on the basis of "the existence of several spiniferous ridges on the testa." Sewell (1926) also distinguished a spiniferous form and found them to be uniformly of a smaller size than Atlantic specimens. In the POFI collections there are also two forms distinguishable on the basis of test differences, the one an echinate form, the other a smooth form; both are small. There are, however, among solitary individuals, intergrading degrees of echination, but conclusions on the validity of Tokioka's variety and form deserve further study, especially of a series of specimens from different oceans.

Although this species is the most common salp of warm seas (Apstein, 1906*a*), it is not one of the better known in regard to test structure. Apstein (1906*a*) figured the echinate aggregate form well, as did Stiasny (1919) and Tokioka (1937). The smooth form of both generations was well figured by Stiasny (1926). It is felt, however, that the figures in the present report are more thorough than previous ones as a result of staining.

Genus *IASIS* Savigny, 1816

Solitary form with five broad, dorsally and ventrally interrupted body muscles and with a broad M C. Aggregate form with five body muscles of which the first is interrupted dorsally and ventrally, the remainder only ventrally; M V is branched into two parts on the right side.

One species, *Iasis zonaria*.

Iasis zonaria (Pallas) 1774

Fig. 30*a-i*

Holothurium zonarium Pallas, 1774: 26.

Salpa polycratica Forskål, 1775: 116.

Biphora zonaria Bruguière, 1789: 182.

Salpa zonaria Chamisso, 1819: 12; Bomford, 1913: 245.

Salpa cordiformis Quoy and Gaimard, 1827: 226.

Salpa microstoma Quoy and Gaimard, 1827: 226.

Salpa unicuspidata Blainville, 1827: 116.

Salpa quadrangularis [?] Lesson, 1830: 268.

Salpa tricuspidata [?] Lesson, 1830: 272.

Salpa cordiformis-quadratica Vogt, 1854: 7.

Salpa cordiformis-zonaria Traustedt, 1885: 382; Oka, 1915: 30.

Salpa nitida [?] Herdman, 1888: 81.

Jasis polycratica Lahille, 1890: 11.

Salpa (*Jasis*) *cordiformis-zonaria* Apstein, 1894*a*: 51.

Jasis zonaria Heider, 1895: 368.

Salpa zonaria-cordiformis Ritter, 1905: 76.

Salpa (*Salpa*) *zonaria* Streiff, 1908: 45.

Salpa (*Iasis*) *zonaria* Metcalf, 1918: 100; Stiasny, 1926: 434; Berrill, 1950: 295.

Salpa (*Jasis*) *zonaria* Sewell, 1926: 88.

Iasis zonaria Ihle, 1935: 527-529; Tokioka, 1937: 223; Thompson, 1948: 132.

SOLITARY FORM: More than 10 specimens examined with length range of 16-51 mm. (Fig. 30*a-e*). *Test:* Firm, elongate; moderately thick; mouth a broad slit; dorsal depression extending to base of upper lip, limited by dorsal limiting elevations; a lateral ridge on each side of latter gradually disappearing anteriorly; posteriorly, lateral ridges ascending to pointed, short, dorsal projections; a posterior ridge extending from the latter ventrally, fusing with its fellow of the opposite side midventrally at the longer, unpaired, median posterior projection; projections prominent in lateral view; a deep lateral groove, or a wide depression as shown by Brooks and Stiasny, gradually forming ventral and anterior to dorsal posterior projections, continuing anteriorly to the front third of body; a ventrolateral ridge extending from gut swelling, coursing anteriorly up to ventral lip; gut swelling moderately large; midventral ridge on posterior region of gut swelling; midventral depression coursing anteriorly from this to base of lower lip; this depression raised slightly in cross section, limited on each side by deep grooves; ventrolateral elevation bearing a ventrolateral ridge (which may be weak)

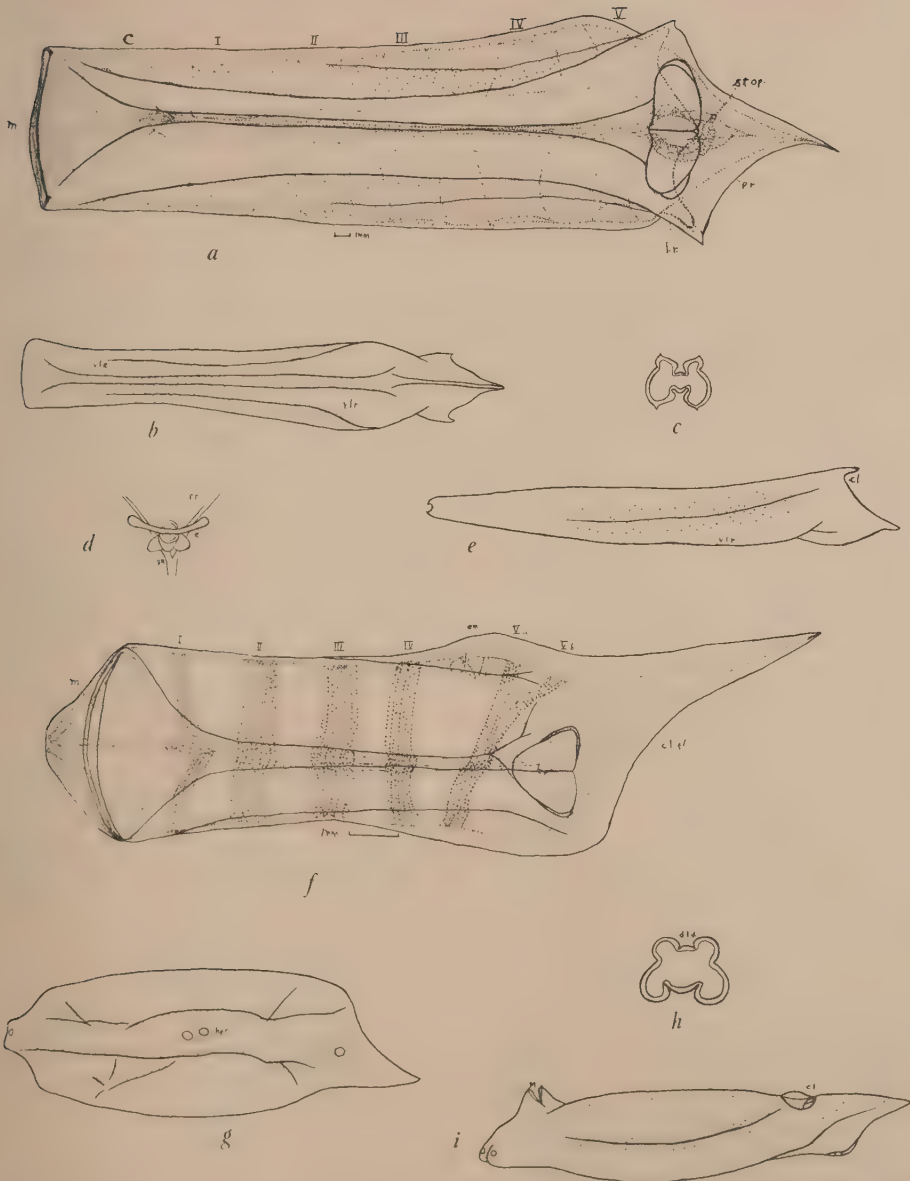


FIG. 30. *Lutis zonaria*. a, Solitary form, dorsal aspect; b, same specimen, ventral surface of test; c, same specimen, schematic cross section of test at level of M III; d, another specimen, dorsal aspect of eye and ganglion; e, same specimen as a, test, left side; f, aggregate form, dorsal aspect; g, another specimen, test, ventral surface; h, schematic cross section of test at level of M IV; i, same specimen as g, test, left side.

swinging outward at level of gut swelling and inward toward anterior third of body; cloacal flap of two fused halves, fringed as in *Thalia democratica*; transverse groove anteriorly at base of flap, posteriorly around cloacal opening. *Muscles*: M C and the five body muscles are broad; all muscles interrupted dorsally and ventrally; M V relatively narrow, extending only a short distance toward ventral surface. *Ciliated groove, ganglion and eye*: Ciliated groove simple, straight, located between the two bow muscles; ganglion and eye between M C and M I; eye may be transversely elongate (Fig. 30d). *Viscera*: Gut in condition D of Ihle and Ihle-Landenberg (1933); stolon forming circle around gut, opening to outside of test by means of a posterior opening just above gut (small in Fig. 30a but may be much larger).

AGGREGATE FORM: More than 10 specimens examined with length range of 19–37 mm. (Fig. 30f–i). *Test*: Asymmetric; consistency as in solitary form; dorsal depression (raised in cross section) with deep groove on each side but without fine median ridge described by Stiasny (1926), extending to base of upper lip; dorsal limiting elevations may bear a weak ridge on each side of depression; anteriorly both lips project dorsally prominently; a prominent chin forming anterior to lower lip; laterally a deep lateral groove (often a broad depression) extending from region of cloacal flap to level of mouth (weak ridges may course above and below this); lips and chin prominent in lateral view; ventrolateral elevation extending posteriorly as a ridge onto posterior projection; gut swelling prominent; on ventral surface, a broad, raised in cross section, midventral depression with a deep groove on each side, extending to chin; limited by ventrolateral elevations; rear projection always on right side, usually long but may be short; a broad, long mantle process extending into posterior projection; attachment organs prominent; two anteriorly directed, one ventrally directed on chin; two midventral, raised on an elevation; three posterior, raised on an elevation of gut swelling.

The number described is the maximum number as reported by Streiff (1908) and Stiasny (1926). Some individuals may deviate from this maximum (Fig. 30g). Further, Stiasny shows two prominent lateral ridges rather than a single lateral groove. He also shows prominent dorsal ridges ("Crista") which are usually only rounded elevations on the specimens examined here, but in general his description is applicable. *Muscles*: Five body muscles (M C is not shown in figure); all interrupted ventrally, M I interrupted dorsally as well; M V dividing into two branches on right side, remaining single on left. *Ciliated groove*: Simple, anterior to M I. *Viscera*: Gut compact, in condition F of Ihle and Ihle-Landenberg (1933); testis projecting as lobules around gut; up to five embryos present dorsally on right between M IV and V.

This species is morphologically one of the best-known salps as its test has a different refractive index than water, even though it is transparent. The test has been figured well by Brooks (1893) and Stiasny (1926) and described in detail by Stiasny.

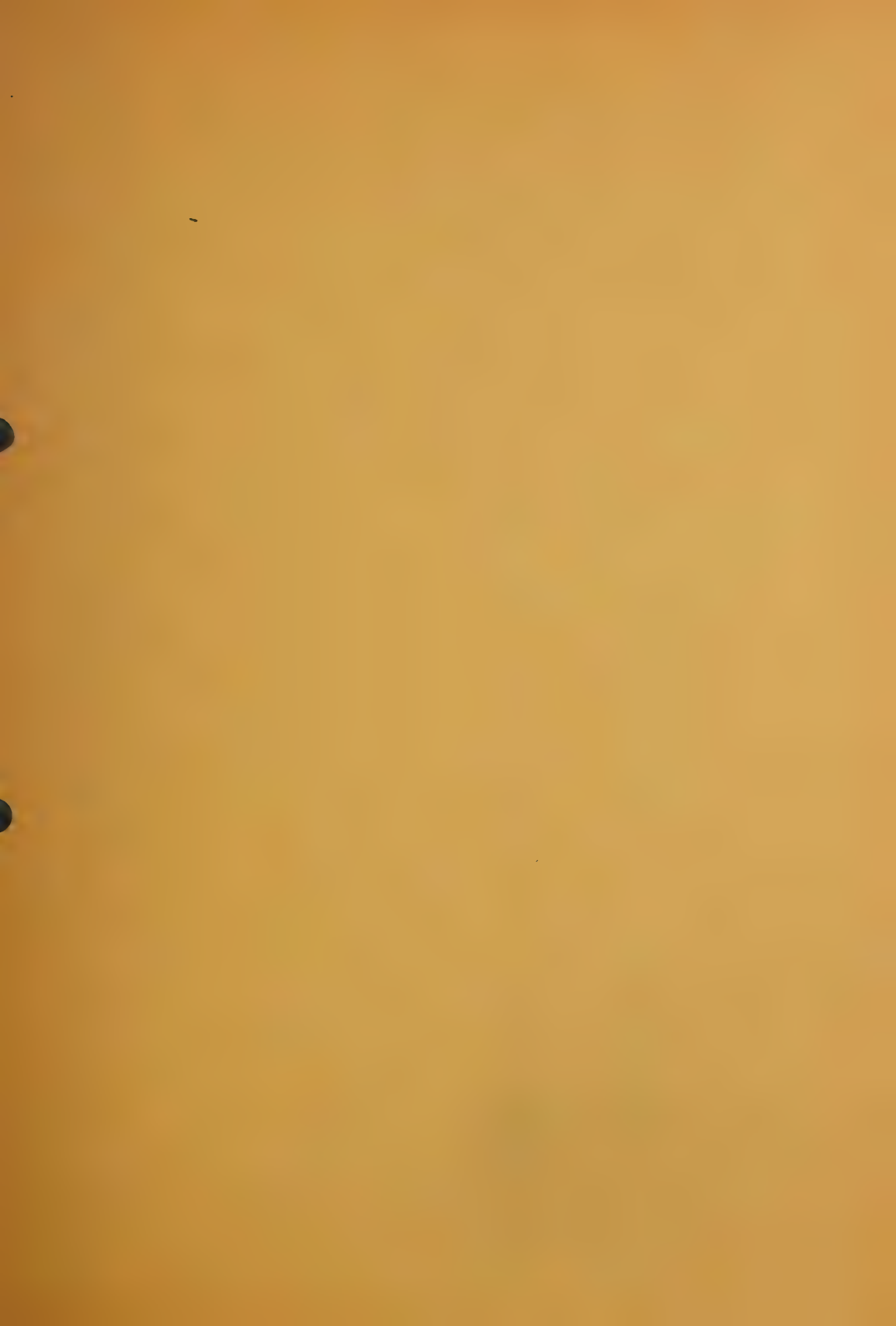
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REACTION OF TUNA TO STIMULI, 1953



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United States Department of the Interior, Douglas McKay, Secretary
Fish and Wildlife Service, John L. Farley, Director

REACTION OF TUNA TO STIMULI, 1953

by

Albert L. Tester
Professor of Zoology
University of Hawaii

Heeny Yuen
Fishery Research Biologist
Pacific Oceanic Fishery Investigations
Honolulu, T. H.

and

Michio Takata
Research Fellow
University of Hawaii



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REACTION OF TUNA TO STIMULI, 1953

By

Albert L. Tester, Heeny Yuen, and Michio Takata

INTRODUCTION

During 1951 and 1952, studies of the response of tuna (mostly "little tunny", Euthynnus affinis) to stimuli were conducted in tanks and ponds of the Hawaii Marine Laboratory at Coconut Island, Oahu, under contract (I6fw-13331 and I6fw-18564) between the University of Hawaii and the U. S. Department of the Interior, Fish and Wildlife Service, Pacific Oceanic Fishery Investigations. The results of these studies (Special Scientific Report: Fisheries Nos. 71, 91, and 130) indicated that the most promising line of attack on the immediate practical problem--discovering a means of attracting tuna to within reach of a fishing vessel at sea--was in the field of chemo-reception. It was found that the tuna in the pond responded positively and often violently to extracts of tuna and other fish flesh, viscera, etc.

In June 1953 another contract (14-19-008-2126) was negotiated to pursue these studies further. The testing of materials in the pond was to be continued. Sea tests were to be conducted to observe the response of "wild" tuna not only to extracts, but also to visual stimuli such as lures of various sizes, shapes, and colors, used either alone or in conjunction with extracts.

This report includes the results of this third study. Although the work was conducted mostly from June to October 1953, sea tests extending from January 29 to November 13, 1953, are included.

ACKNOWLEDGMENTS

As in past years, troll fishing to stock the ponds with tuna was conducted under the skillful direction of Mr. Lester Zukeran, skipper of the University of Hawaii research vessel Salpa. Mr. Eugene Nakamura and Mr. Royden Ikeda, students, assisted in both fishing and sea testing with this vessel. Mr. Charles Nakamoto, assistant to the Hawaii Marine Laboratory, again was responsible for the feeding and care of the captive fish.

We are again indebted to Mr. Raoul Pantaleoni of E. I. Du Pont de Nemours & Company, to Dr. Ernst T. Theimer of van Ameringen-Haebler, Inc., to Mr. George H. Zirkel of P. R. Dreyer, Inc., and to Mr. R. E. Horsey of Sindar Corporation for supplying many of the chemical compounds which were tested in the pond. In particular, we are grateful to Mr. Fritz Jermann of Hawaiian Tuna Packers Ltd. for preparing most of the extracts which were tested at sea.

The staff of the Pacific Oceanic Fishery Investigations cooperated to the utmost. Special thanks are due Mr. O. E. Sette, Director, and Mr. D. L. McKernan and Dr. W. F. Royce for advice and assistance. Not only were the two research ships Charles H. Gilbert and Hugh M. Smith made available for sea testing, but also many of the staff members conducted or assisted in conducting the sea tests, including D. L. McKernan, J. Slipp, D. Yamashita, H. Mann, and T. Otsu.

The senior author, who directed the investigation, assumes responsibility for the compilation of this report and for the analysis and interpretation of the data which are included. Most of the sea testing was undertaken by the second author; most of the pond testing was undertaken by the third author.

POND AND TANK EXPERIMENTS WITH EXTRACTS OF FOOD AND OTHER MATERIALS

Catching and Establishing the Fish

Two little tunny (Euthynnus affinis), originally established during the summer of 1952 in the large Pond No. 5 at Coconut Island (Tester et al. 1954) survived the winter and formed the nucleus of a new population which was established during July and early August 1953. To the two survivors were added 12 tunny and 9 yellowfin (Neothunnus macropterus) at the end of June. As in the previous year, the fish were caught by trolling with the Salpa and were transported in the vessel's livewell to Pond No. 5. Of the 21 fish introduced to the pond only one, a tunny, failed to become established, that is, to start feeding. This great success, compared with that of previous years, is attributed to the presence of the two survivors, which acted as leaders of the new fish.

Mortality among the established tunny was moderate between July 1 and October 1, 1953: 5 of the 13 died, leaving 8 which have survived to the time of writing (January 1954). Although the 9 yellowfin appeared to be in good condition at the time they started feeding, all had died by the middle of September. The reason for this mortality, which took place irregularly throughout the period, is unknown.

Two tunny originally established during the summer of 1952 in a concrete tank (Tester et al. 1954) survived the winter and were used in experiments during the early summer. One jumped from the tank and died on July 19, 1953. The other, which was partially blind, died 3 days later.

Feeding the Fish

From April 25 to July 17, 1953, the tunas in the pond were fed exclusively on frozen squid from the mainland. They were fed 4 times a week (Tuesday, Thursday, Saturday, and Sunday) at a rate of about 2 pounds of squid per fish per week. Following July 17, 1953, they were fed daily for 1 week on squid, 1 week on skipjack flesh, 1 week on frozen shrimp from the mainland, and thereafter 4 times a week on skipjack flesh. The change in diet was associated with experiments (to be discussed later) probing the possibility of food-conditioned responses.

The tunny in the tank were fed on tuna flesh 4 times a week throughout 1952 and until they died in 1953.

Materials and Testing Procedures

One hundred and sixty-nine experiments were conducted during the summer of 1953, 162 in the pond and 7 in the tank. Of these, 94 involved extracts of "natural" foods and the other 75 involved solutions or suspensions of chemical materials. Pertinent data on these tests are included in the appendix to this report. The tests are numbered in sequence with those presented in appendix I of Tester et al. (1954). They are referred to by number in the sections which follow, e.g. #495.

"Natural" foods from which extracts were made included skipjack (Katsuwonus pelamis) flesh, skipjack viscera, skipjack blood, dolphin (Coryphaena hippurus) ovaries, anchovy (Stolephorus purpureus), hammerhead shark (Sphyrna sp.) flesh, mainland squid, mainland shrimp, and marine plankton. The materials were prepared in a similar manner: fish, squid, or shrimp flesh was chopped either by hand or in a grinder, placed in a Waring Blendor and macerated after adding tap water, further diluted with water, and allowed to stand for several hours in a refrigerator. Either the whole extract was tested, or the clear portion was separated by decanting or centrifuging and tested. The procedure was the same for blood and plankton except that the initial chopping was not necessary. A self-digested skipjack viscera preparation supplied by Hawaiian Tuna Packers Ltd. was also used in preliminary tests. In some preparations 95-percent ethyl alcohol, instead of water, was added prior to maceration in the Blendor.

The miscellaneous chemical materials were dissolved or suspended in water before testing, using Tergitol and/or mechanical emulsifier when necessary.

Tank and pond tests were conducted in a similar manner to that of last year (Tester et al. 1954). The only important change involved the pond: the observation tower was moved from the western end to the center of the north side (fig. 1). In brief, testing was conducted as follows: the fish were timed and counted in an attraction area during five 3-minute control periods (2-minute periods in the tank); the test material was introduced from the top of the tower into the attraction area through a stream of water which flowed constantly; and the fish were timed and counted during ten subsequent 3-minute test periods. "Timing" consisted of recording on an electric clock operated by a push switch the number of seconds spent by one or more individuals of the tunny school in the attraction area. The "attraction area" was a portion of the pond in front of the tower which was marked off by two pieces of string stretching across the pond; it was approximately 39 by 75 feet in area. "Counting" consisted of recording on a hand counter the number of passes made by each fish in the attraction area while the fish was moving in either a "down" or "up" (easterly or westerly) direction. Materials introduced through the pipe leading from the top of the tower remained in the attraction area for at least 15 minutes and then gradually dispersed. The time and direction of dispersal was governed by the strength and direction of the weak tidal current. Usually a period of at least 30 minutes was allowed to elapse between the end of one experiment and the start (control conditions) of the next to enable introduced materials to disperse or to become diluted to a level well below the threshold of response.

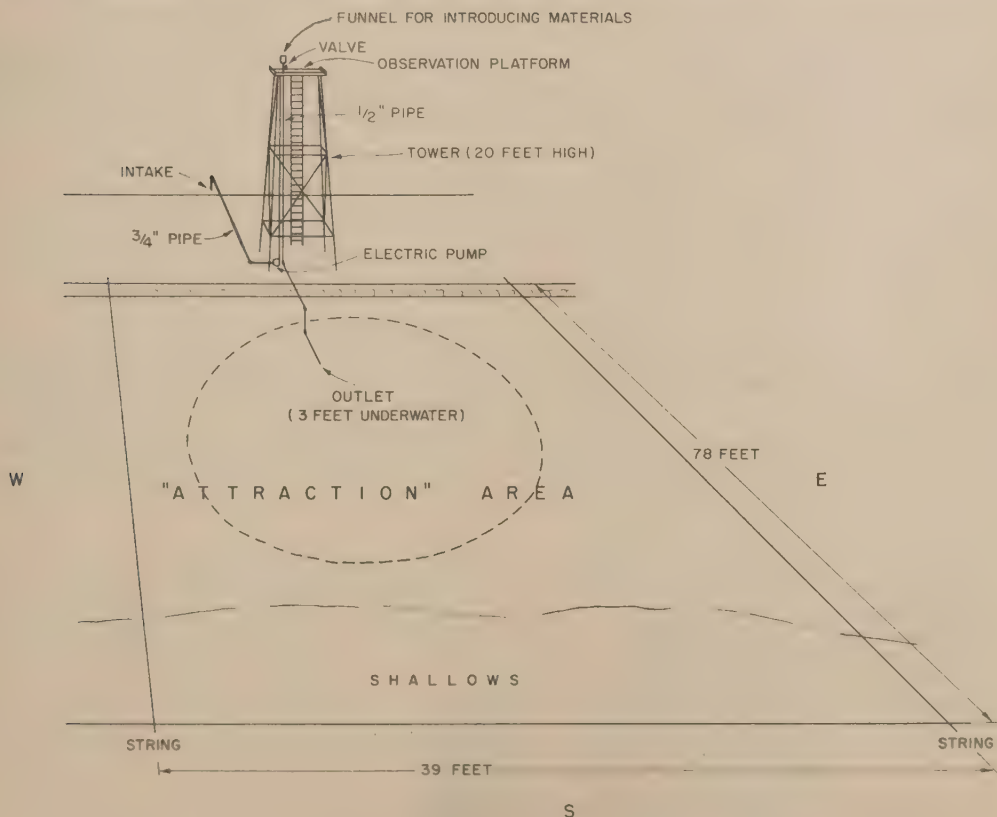


Fig. 1.--Diagram of Pond No. 5 at Coconut Island showing the observation tower, attraction area marked off with string, and the pipes, pump, and funnel used to introduce test materials to the pond.

In addition to obtaining quantitative data in the manner described above, the observer also recorded his visual impression of the strength of the response in one of five categories indicated as "-", an apparent repulsion; "0", no response; "X", a weak positive response; "XX", a moderate positive response; and "XXX", a strong positive response.

Quantitative data were obtained only with the tunny. Yellowfin were also present in the pond, but no attempt was made to measure their reactions because of their erratic behavior. It might be noted, however, that when they did enter the attraction area during an experiment, their response was similar to that of the tunny except that it was generally less pronounced for a given stimulus.

Response to Extracts of "Natural" Food Substances

Although the tunny in Pond No. 5 had been fed exclusively on mainland squid for about 2 months prior to July 1, 1953, before their diet was changed they showed a positive response to extracts of skipjack viscera (#362, but not #357, 358, 363, 368), skipjack flesh (#359, 360, etc., but not #367), skipjack blood (#383), dolphin ovary (#377), anchovy (#384, but not #396), hammerhead shark flesh (#393, but not #373), mainland shrimp (#374, 375), mainland squid (#370, 376, etc.), and marine plankton (#387). The two tunny in the concrete tank, which had been fed exclusively on tuna flesh, showed a positive response to extracts of skipjack flesh (#378, 389), anchovy (#385), mainland shrimp (#382, 386), mainland squid (#380), but not to an extract of hammerhead shark flesh (#392).

In general, the response in the pond was weak and extremely variable as compared with that obtained with extracts of tuna flesh, viscera, etc. in the summer of 1952. To produce responses with tuna flesh extract it was necessary to use about five times as much material as was used in the summer of 1952 (about 100 g. as compared with about 25 g. of flesh). However, the amount used was not as much as was necessary during the spring of 1953 (about 350 g.), when the two surviving tunny were particularly unresponsive (Tester et al. 1954).

The fact that the squid-fed tunny did respond to such a wide variety of extracted food substances (even to plankton in one experiment) indicated that they were not conditioned to the smell or taste of the particular food which was being fed. However, at times, it seemed that the response of the pond tunny to squid extract was more pronounced than that to extracts of other substances.

It was decided to undertake a series of experiments involving three test substances (extracts of squid, skipjack flesh, and shrimp), each to be tested on each of three days per week (Tuesday, Wednesday, and Thursday), the tests to run for 3 consecutive weeks. Prior to and during each successive test period the food was to consist respectively of squid, skipjack flesh, or shrimp. Each week one of these foods was to be fed to the fish at 4 p.m. each day from Thursday (after the Thursday tests were made) to the following Wednesday. The order of testing was to change each day, so that no two tests would appear in the same order on successive days of each week (Latin square design).

Two departures from the plan were made. Due to an error, the same order of testing was used in two of the three days in Week 1. A fourth substance was added to the three primary tests, namely, a blend (equal parts) of squid, skipjack flesh, and shrimp extract. Thus two tests were made in the morning and two in the afternoon of each day. The series either started or ended with the blend, which was either preserved or not preserved with sodium bisulphite. A summary of the results is given in appendix I (#398 to 409; #414 to 425; and #436 to 447). It will be noted that in each test the same method of preparation and the same amount of material was used (100 g. extracted with 2,000 ml. water).

For each test the strength of the response according to the observer's visual impression and also the strength of the response as measured quantitatively is given in table 1. The variate for the latter, which was used for statistical analysis, may be explained by means of an example. In the experiment conducted with an extract of skipjack flesh on Thursday of the second week, when the fish had been fed skipjack flesh (see table 1, E₂D₃F₂), the mean time spent by the fish in the attraction area was 7.2 seconds during control periods and 28.6 seconds during test periods, with a mean difference of 21.4 seconds. The mean number of "passes" in the attraction area was 4.4 during control periods and 15.2 during test periods, with a mean difference of 10.8 passes. The differences in both time and count reflect the response, although their relative value as a measure of response is difficult to assess. The two were added, giving 32.2; rounded off, giving 32; and increased by 20, giving 52. The last step, adding 20, was included because in some cases negative differences were obtained, i.e., the fish spent relatively more time and/or made more passes in the attraction area during control than during test periods.

Order of testing is not indicated in table 1. Inspection of the data indicated no consistent trends in response with order of testing within days: on some days the first substance tested gave a high response whereas on other days the last substance tested gave a high response. Similarly, inspection of the data indicated no significant differences between the preserved and non-preserved blend. Accordingly the results were analyzed in toto according to three criteria of classification:

- (1) Extract -- E₁-squid; E₂-skipjack; E₃-shrimp; E₄-blend
- (2) Days -- D₁-Tuesday; D₂-Wednesday; D₃-Thursday
- (3) Food (= Weeks) -- F₁-squid; F₂-skipjack; F₃-shrimp

Table 1.--The response of tunny to four extracts (E) on three days (D) in each of three weeks during which they were fed three different foods (F). For further explanation see text.

Food	Days	Extract				Total
		E ₁ Squid	E ₂ Skipjack	E ₃ Shrimp	E ₄ Blend	
F ₁ squid	(D ₁ Tue.)	44(X)	49(XX)	21(X)	62(XXX)	176
	(D ₂ Wed.)	29(X)	30(XX)	29(X)	57(XXX)	145
	(D ₃ Thurs.)	35(X)	52(XXX)	12(O)	41(XX)	140
		108	131	62	160	461
F ₂ skipjack	(D ₁ Tue.)	43(XX)	49(XX)	57(X)	24(X)	173
	(D ₂ Wed.)	27(X)	56(XX)	34(X)	23(X)	140
	(D ₃ Thurs.)	9(O)	52(X)	32(X)	31(XX)	124
		79	157	123	78	437
F ₃ shrimp	(D ₁ Tue.)	44(XX)	36(XX)	48(X)	27(X)	155
	(D ₂ Wed.)	28(X)	32(XX)	36(X)	51(XXX)	147
	(D ₃ Thurs.)	5(X)	26(X)	10(O)	23(O)	54
		77	94	94	101	366

The analysis is as follows:

Source of variation	Degrees of freedom	Sum of squares	Mean square
F	2	405.723	202.861
D	2	1304.889	652.444**
E	3	995.334	331.778*
FxD	4	467.944	116.986
FxE	6	2240.499	373.416*
DxE	6	968.000	161.333
FxDxE	12	1139.167	94.930

where * indicates an F value for which P is less than 0.05, and ** indicates an F value for which P is less than 0.01, in all cases using the second order interaction as the error term.

There are no significant differences among the mean responses to the different foods which were fed. However, as shown in the following values of the grand means, there is a general decrease from Week 1 (F₁) to Week 3 (F₃): 38.4, 36.4, 33.2. In view of the results which follow, this trend, if real, is more likely related to time than to food. Of necessity, time (weeks) and food are confounded in the design.

There are highly significant differences in the mean responses of the fish between successive days of the week. As shown by the grand means for successive days, there is a progressive decrease in response from D₁ (Tuesday) to D₃ (Thursday): 42.0, 36.0, 27.3. The decrease is consistent within weeks, as is apparent from the lack of any significant interaction involving days in the analysis of variance table, or as may also be seen from the data of table 1. It may be shown that the regression of response on days is highly significant (mean square for regression is 1290.667**) and accounts for most of the variation between days. A study of tidal heights, direction of tidal current, and weather at the time of each test revealed no apparent relationship to account for the regression. It is most likely due to progressively increasing fatigue or a dulling of response with successive testing. It may reflect a learning process--the fish can be deceived into a feeding reaction by the extract but become less responsive when they find that no food is available^{1/}. Although the fish were allowed to rest on Saturdays and Sundays, the regression may have been carried over from one week to the next, particularly if it involved a progressive dulling of response or a learning process, thus accounting in part at least for the decrease in response between weeks noted in the preceding paragraph.

There are significant differences in the responses to the various extracts. The grand means for squid, skipjack flesh, shrimp, and blend extracts are respectively as follows: 29.3, 42.4, 31.0, 37.7. According to these results the skipjack flesh extract gave the greatest response and the squid extract the smallest response, with the blend slightly greater than the mean of the other three. Although heterogeneity is indicated, it may not reflect differences in response between the substances *per se*, but rather an interaction between the extracts and the food fed (no significant differences between the grand means for extracts are indicated if the FxE interaction is used as the error term).

There is a significant first order interaction between extracts and foods (or weeks). This indicates that the fish responded differently to the four extracts when they were fed on different foods (or, in different weeks). The nature of the differential response may be seen from the following summary, which gives the mean response according to both food and extract:

^{1/} This has been suspected to occur between successive tests within days on other occasions.

Food (Weeks)	Extract			
	E ₁ (squid)	E ₂ (skipjack)	E ₃ (shrimp)	E ₄ (blend)
F ₁ (squid)	36.0	43.7	20.7	53.3
F ₂ (skipjack)	26.3	52.3	41.0	26.0
F ₃ (shrimp)	25.7	31.3	31.3	33.7

It is unfortunate that the effect of food cannot be separated from the possible effect of the time component (Weeks), although it is difficult to see how the latter, if a regression, could lead to a significant interaction with extract. The inclusion of the blend extract data has contributed to the interaction. However, the interaction is still significant if these data are excluded from the calculations. The response to squid extract was greatest when the fish were being fed squid. The response to skipjack extract was greatest when the fish were being fed skipjack. The response to shrimp extract was greatest when the fish were being fed skipjack, but it was greater when they were fed shrimp than when they were fed squid. The differential response indicates a degree of conditioning of the fish to a particular food substance. In part, this may explain the weaker responses to skipjack flesh and viscera extracts during July 1953 as compared with the summer of 1952, for in 1953 they were being fed squid whereas in 1952 they were being fed tuna flesh.

On completion of the experiments on conditioning the tunny were fed skipjack flesh three times a week. Additional experiments indicated no significant difference in response between extracts of light red (#469, 473, 478, 484) and dark red (#470, 472, 480, 482) skipjack flesh.

Alcohol extracts of skipjack flesh seemed to elicit a much weaker response than aqueous extracts (see #475 to #489). This was the case when the alcohol extracts were tested without further processing and also when they were evaporated to dryness and redissolved in water. The reason may be that the "attractant" was only partially extracted with alcohol; this was suspected to be true in some of the preparations used in 1952-53 (Tester et al. 1954).

Response to Chemical Compounds

The following chemicals in solution or suspension were tested during the summer of 1953:

Adenylic acid, muscle (#517)	Ionine C-1 (#506)
Alanine, alpha DL (#450)	Isoeugenol (#410)
Amyl caproate (#505)	Lactalbumin (#521)
Amyl cinnamate (#372)	Leucine, DL (#430)
Anethol (#427)	Liver extract concentrate (#499)
Anisic aldehyde (#365)	Liver fraction "L" (#497)
Arginine monohydrochloride, L (#428)	Lysine monohydrochloride (#466)
Asparagine, DL (#426)	Lysine monohydrochloride, L (#451)
Aspartic acid, L (#453)	Mercaptan, phenyl ethyl (#516)
Aspartic acid, DL (#463)	Methionine (#390)
Astrotona (#515)	Musk ambrette (#503)
Bologna flavor (#411)	Musk ketone (#498)
Betaine (#474)	Musk xylol (#504)
Blood fibrin (#523)	Norvaline, DL (#456)
Butter flavor (#413)	Ornithine monohydrochloride, DL (#468)
Butyric acid, alpha amino n (#455)	Phenylalanine (#491)
Cadaverine dihydrochloride (#500)	Phenyl ethyl alcohol (#509)
Calcium pantothenate, D (#493)	Proline, L (#467)
Casein (#512, 524)	Pyridoxine hydrochloride (#462)
Casein hydrolysate (#522)	Riboflavin (#510)
Chlorophyll (#459)	Serine, DL (#429)
Cholic acid (#496)	Sodium bisulphite (#449)

Citral (#371)	Testosterone (#501)
Creatinine (#495)	Threonine, DL (#461)
Eucalyptol (#395, 513)	Threonine, DL, with allothreonine (#460)
Glutamic acid hydrochloride, L (#519)	Thiamine hydrochloride (#492)
Glutamic acid monohydrate, DL (#452)	Tonquin musk (#511)
Glutaric acid, alpha keto (#431)	Tryptophane (#434)
Gluten (#525)	Tryptophane, DL (#458)
Glycyl-glycine (454)	Tyrosine, DL (#490)
Guanine (#435)	Uracil (#494)
Guanine hydrochloride (#464)	Urami (#465)
Hexahydrobenzoic acid (#518)	Vioosterol (irradiated ergosterol) (#507)
Histidine (free base) (#448)	Vitamin A, crystalline (#514)
Histidine monohydrochloride, DL (#432)	Yeast hydrolysate (#520)
Hydroxyproline (#433)	Xanthophyll oil (#457)
Ionine, alpha methyl (#508)	

There was no positive response to any of the above substances. In a few (#365, 413, 498, 503), activity simulating a response was noted, but this may have been caused by extraneous factors or it may have been a curiosity about or sensing of some of the strong smelling materials. In others of a bright orange color (#510) or a dark green color (#459) there was an avoiding or repellent effect which was obviously visual in origin.

Discussion

In view of the results given in a preceding section which indicate that the response to extracts of "food" substances may be partially conditioned by the particular type of food fed, it seems worthwhile to speculate further on the part which conditioning may play in causing all responses in the pond. The so-called "attractant" to tuna may be a complex of substances which are present in one grouping or another, and to a greater or lesser extent, in extracts of many marine animals such as fish, squid, shrimp, or even plankton. Certainly the tuna in the pond have become accustomed to being fed on dead material--so much so that they ignore live bait in the pond. Possibly they have associated the act of feeding with the smell or taste of this "attractant" which is released into the water from the cut-up food material when it is thrown to them at feeding time. Thus they may exhibit a conditioned feeding response when stimulated by this "attractant" which is present in the extract. This would be a possible explanation of why they respond to extracts of one material when another is being fed. In addition, a further conditioning to a particular substance or complex of substances in a particular food organism could conceivably take place. If so, this would explain why they show a heightened response to extracts prepared from the particular food substance which they are being fed. It was hoped that even if this were so, wild fish at sea might be naturally "conditioned" to a smell given off by the whole, live organisms on which they feed, particularly if the organisms were occasionally injured during the feeding process and gave off attractive body juices. More information on the part played by conditioning, natural or otherwise, might be obtained from pond experiments if the tunny would feed on live bait. As they will not do this (unless the bait is caught and thrown to them), the only other obvious way to settle the question is to present the extracts to wild fish at sea and to study their response.

POND EXPERIMENTS WITH EDIBLE LURES

As the tuna in the pond were accustomed to being fed with materials thrown to the surface by an attendant, they showed a strong visual response to objects which suddenly appeared on the surface and also to persons who approached the edge of the pond. This conditioned behavior made it difficult to perform meaningful experiments in the field of visual and visual-chemical stimulation (Hsiao and Tester 1954). Inedible objects such as leaves falling to the surface or stones thrown to the surface would attract the fish if they were within about 50 feet of the object (the tunny have a keen sense of vision). They would dash after such objects, snap at them, and sometimes take them into their mouths but, as nearly as could be observed, would then reject them. It would have been possible to devise experiments to study the response to inedible objects of different

materials, buoyancy, size, shape, and color to see if there was any preference, but this was not done for fear that if these artificial lures were made sufficiently attractive to be taken by the fish they might be eaten and would cause their death. To avoid this possibility edible lures were used. A series of 33 pond experiments were conducted over the period from August 18 to October 29, 1953. These are discussed in the following sections.

Materials and Methods of Preparation

In view of the practical problem of attracting tuna to the stern of a fishing vessel, there was need for an edible material which was low in cost, easily prepared, and at the same time both visually and chemically attractive to the fish. In other words it was desired to create a lure which was attractive in shape, size, color, and movement in order to visually attract the fish from a distance, and which at the same time was edible and sufficiently palatable to induce them to want more. Three basic materials were tested: (1) gelatin capsules, (2) macaroni, and (3) agar gelatin.

The gelatin capsules (Eli Lilly & Co., No. 000) were about 1 inch long when closed, and consisted of two parts, the body (about 7/8 inch) and the cap (about 5/8 inch). They gradually softened in water, eventually collapsing and dissolving after several minutes. Unsuccessful attempts were made to impart motion to the whole capsule. A slow motion was imparted to the open-ended body or cap when floating on the surface by (a) gluing pellets of calcium carbide inside the closed end, (b) gluing pellets of "Bromo-seltzer" inside the closed end, and (c) stuffing the body or cap loosely with cotton wool (to form an adsorption surface) and filling with 95-percent alcohol (extract of skipjack flesh) before throwing to the surface of the water. The motion of the first two depended on gas production on contact with sea water for the propelling force; that of the third depended on the affinity of alcohol for water. The motion was very slow, of the order of about 6 inches per second or less. The carbide-filled capsules were not used in the pond for fear of killing the fish.

Some of the gelatin capsules were coated with a sticky glue (plastic in acetone) and were then dusted with aluminum powder (Sirius Commercial Aluminum Compound) to make them silvery in appearance. Others were coated with a gummy concentrate of skipjack extract (boiled to a residue) giving them a brownish color. Still others were coated with both the aluminum and the concentrate. They were tested both with and without the motion imparted by the chemicals.

The precut macaroni ("Royal" or "Golden Grain") was cooked in water, in concentrated skipjack extract, and in concentrated anchovy extract, in some cases both with and without preservative (about 2 percent sodium bisulphite). The cooked pieces were about 3/8 inch in diameter and 1-1/2 inches long.

The amount of extract used in cooking each small batch was adjusted so that all was absorbed by the time the macaroni was cooked to the right consistency. The pieces were then removed from the pot with a spatula and dried on a screen until they were slightly sticky to the touch. Before being used some were coated with corn starch to keep them from sticking together; others were coated with aluminum powder to give them a silvery appearance. Some were plugged at both ends with glue or with small pieces of cotton wool so that they tended to float when thrown to the surface; others, not plugged, would slowly sink.

Agar (common Japanese variety) was purchased in long strips (about 11 x 1 x 1 inches). Both "colorless" and red varieties were used. It was boiled with water (300 ml. to one strip), concentrated skipjack extract, and concentrated anchovy extract, both with and without the addition of aluminum powder and both with and without preservative. The boiled solution was poured into flat pans and set in the refrigerator. It was then removed and sliced into strips approximately 2 x 1/4 x 1/16 inches. Strips thicker than 1/16 inch tended to sink too rapidly; those thinner than 1/16 inch tended to float on the surface of the water.

Method of Testing

In the first experiment, the edible lures were thrown to the fish in the pond from ground level after the school had gathered in front of the observer. As the fish were visually attracted to the observer as well as to the lures this method was abandoned. In all subsequent experiments the lures were thrown to the pond from the tower when the tunny were away from but approaching the attraction area. Generally the fish did not see the splash of the lures as they hit the water, but saw the lures themselves on entering the attraction area. Observations were made of the number of lures which sank before the fish approached (classified as "not seen"), the number presumably visible to the fish but ignored ("ignored"), the number taken into the mouth but rejected or spat out ("rejected"), and the number taken and eaten ("eaten"). Observations were made also on the behavior of the fish, e.g., whether they showed excitement and whether they returned to the attraction area after the lures were presented. In later experiments the response was indicated in the same categories as were used in the experiments with chemical stimulation (0 to XXX).

Each experiment took a considerable period of time (usually about 30 minutes); it could be performed only when the tunas were cruising regularly up and down the pond. Only a few lures (usually three with one observer or up to eight with two observers) could be presented to the fish at one time; if more were used it was difficult to keep track of the ultimate fate of each.

Results

Four experiments were performed with gelatin capsules, using about 12 capsules in each and presenting them two or three at a time to the fish. In the first, the capsules were coated with aluminum powder, plugged with cotton, and motivated with alcohol extract. In the second, they were coated with aluminum powder and extract concentrate, plugged with cotton, and motivated with alcohol extract. In the third, they were coated with aluminum powder and extract concentrate, and motivated with Bromo-seltzer. In the fourth, they were coated with extract concentrate only, and motivated with Bromo-seltzer. In the first experiment, the fish were attracted to the capsules, took them into their mouths, but then rejected them. In the other three experiments they were attracted to and ate all the capsules. Thus it seems that all preparations were visually attractive to the fish, but only those coated with extract concentrate were actually eaten. The small amount of motion imparted to the capsules by the alcohol and Bromo-seltzer appeared to play little or no part in attraction.

In 14 experiments performed with macaroni lure preparations there was no noticeable difference in response to materials which were (1) either preserved in sodium bisulphite, or not; (2) either plugged with cotton wool, or not (although more of the latter sank before being observed by the fish); and (3) either cooked in concentrated skipjack extract or cooked in concentrated anchovy extract. The data grouped into four main categories are included in table 2.

It is noteworthy that the pond fish consumed 54 percent of the plain macaroni lures; however, these were usually eaten only towards the start of a series of experiments. The results suggest that coating with aluminum powder increases the visual attractiveness of the lure, that coating with extract increases its chemical attractiveness or palatability, and that a combination of the two gives the best response, with 95 percent of the lures being eaten. However, only in the comparison of "with aluminum and extract" versus "plain" is the difference in response statistically significant^{2/}.

In 13 experiments with agar lure preparations, there was no noticeable difference in response between preparations with or without the preservative nor between preparations boiled in concentrated skipjack or anchovy extract. Plain red agar strips seemed to be more attractive than plain colorless agar strips, but the difference was not statistically significant. The results grouped in four categories are included in table 2.

^{2/} Testing the ratio (ignored plus rejected): (eaten) yields an adjusted Chi-square of 13.8 with one degree of freedom (P less than 0.01).

Table 2.--Summary of the response of tunny to pieces of cooked macaroni and strips of agar in several experiments

Lure and preparation	Number of pieces				Total	Percent eaten
	Not seen	Ig-nored	Re-jected	Eaten		
Elbow macaroni:						
Plain	(7)	2	9	13	24	54
With aluminum	-	-	4	10	14	71
With extract	(1)	1	3	7	11	64
With aluminum and extract	(4)	1	1	40	42	95
Agar strips:						
Plain	-	3	6	10	19	53
With aluminum	-	2	5	2	9	22
With extract	(2)	1	-	22	23	96
With aluminum and extract	(3)	1	3	11	15	73

The best response, with 96 percent of the lures being eaten, was obtained with agar strips cooked in concentrated extract. As they assumed a brownish color, they may have been visually as well as chemically more attractive than plain colorless agar. The addition of aluminum did not seem to increase the attractiveness of the agar preparations.

A series of tests was conducted to determine if there were any differences in response to (a) macaroni cooked in concentrated skipjack extract and coated with aluminum powder, and (b) agar cooked in concentrated skipjack extract and impregnated with aluminum powder. In both cases the preparations, part of a large quantity used in sea tests, were preserved with 1 percent sodium bisulphite. The lure preparations were presented alternately to the fish, eight pieces at a time. The pairs of tests were repeated several times throughout the morning, and again throughout the afternoon of the same day. The results are shown in tables 3 and 4.

In the morning series (table 3) the tunny ate 69 percent of the macaroni lures and 100 percent of the agar lures. In the afternoon series (table 4) they ate only 10 percent of the macaroni lures but still ate 100 percent of the agar lures. It is obvious from the data, and it was still more obvious from observation, that the pond fish showed a decided preference for the agar lures after the first pair of tests. The percentage of macaroni lures which was eaten gradually decreased with successive testing. In the last three pairs of tests in the afternoon some of the pieces of macaroni were taken into the mouth, but all were rejected; on the other hand all agar strips, if seen, were eaten. Apparently a learning process was involved. In general, the overall reaction (speeding, surfacing, splashing, return to area, etc.) was more pronounced with the agar than with the macaroni lures; the difference was more noticeable in the morning than in the afternoon tests.

Table 3.--Results of experiment (#32--a.m.) with macaroni and agar preparations, eight pieces of each presented alternately in a series of tests

Lure and preparation	Test No.	Number of pieces				Total	Percent eaten	Reaction
		Not seen	Ig-nored	Re-jected	Eaten			
Elbow macaroni: plus aluminum and extract	1	(8)	-	-	-	-	-	XX
	3	-	-	-	8	8	100	XX
	5	-	-	1	7	8	88	XX
	7	-	1	-	7	8	88	XX
	9	-	5	-	3	8	38	X
	11	(pieces not visible due to reflection of sun)				-	-	XX
	13	-	1	-	7	8	88	X
	15	(8)	-	-	-	-	-	
	17	-	4	-	4	8	50	XX
	18	-	3	-	5	8	62	X
	19	-	5	-	3	8	62	X
Totals		(16)	19	1	44	64	69	
Agar strips: plus aluminum and extract	2	-	-	-	8	8	100	XXX
	4	(1)	-	-	7	7	100	XX
	6	-	-	-	8	8	100	XX
	8	-	-	-	8	8	100	XX
	10	-	-	-	8	8	100	XX
	12	-	-	-	8	8	100	XX
	14	-	-	-	8	8	100	XX
	16	-	-	-	8	8	100	XX
Totals		(1)	-	-	63	63	100	

Table 4.--Results of experiment (#33--p.m.) with macaroni and agar preparations, eight pieces of each presented alternately in a series of tests

Lure and preparation	Test No.	Number of pieces				Total	Percent eaten	Reaction
		Not seen	Ig-nored	Re-jected	Eaten			
Elbow macaroni: plus aluminum and extract	1	-	2	3	3	8	62	X
	3	-	3	4	1	8	12	X
	5	-	4	3	1	8	12	X
	7	-	2	6	-	8	0	X
	9	-	4	4	-	8	0	X
	11	-	6	2	-	8	0	X
Totals		-	21	22	5	48	10	
Agar strips: plus aluminum and extract	2	-	-	-	8	8	100	XX
	4	-	-	-	8	8	100	X
	6	-	-	-	8	8	100	X
	8	(1)	-	-	7	7	100	X
	10	-	-	-	8	8	100	X
	12	(2)	-	-	6	6	100	X
Totals		(3)	-	-	45	45	100	

Discussion

The pond tests showed that tunny held in captivity would eat edible preparations such as gelatin capsules, pieces of macaroni, and strips of agar gelatin, and that these were more avidly consumed if they were made chemically attractive, or palatable, with concentrated extracts of skipjack or anchovy. In some cases, the relative number eaten seemed to depend, in addition, on the visual attractiveness of the lures.

The pond fish showed a distinct preference to agar preparations over macaroni preparations after the first pair of trials: a learning process seemed to be involved. The reason for the preference is uncertain, but it probably involved a difference in smell, taste, or texture of the materials. Although the two preparations were basically different in composition (macaroni is a starch and agar is a sulphuric acid ester of galactan), both were thoroughly impregnated with the same concentrated extract of skipjack flesh, and presumably should have had a similar smell or taste. Perhaps the considerable difference in texture between the macaroni and agar preparations was responsible for the choice: the strips of agar were softer, more pliable, and more "jelly-like" than the pieces of macaroni.

Although there was no assurance that sea fish would respond in a similar manner to the pond fish (which were accustomed to feeding on dead, non-motile food), it was considered worthwhile to conduct sea tests with edible lures. Unfortunately, attempts to induce appreciable motility in edible lures have been unsuccessful to date. As will be discussed later, motility may be an important factor in the successful use of either edible or inedible lures to attract tuna at sea.

SEA TESTS WITH EXTRACTS

Preparation of Material

For the most part the extracts used in the sea tests were prepared in 50-gallon drums by Mr. F. Jermann of Hawaiian Tuna Packers Ltd. The materials are briefly described as follows:

- (1) Skipjack viscera, ground, steam-cooked, water added, filtered, preserved with 2 percent sodium bisulphite (demijohns - 1/20/53).
- (2) Yellowfin flesh, ground, extracted with water, filtered, and preserved with 2 percent sodium bisulphite (Drum No. 1 - 2/18/53).
- (3) Yellowfin flesh, as above (Drum No. 2 - 2/24/53).
- (4) Yellowfin flesh, as above (Drum No. 3 - 3/4/53).
- (5) Skipjack viscera, ground, extracted with water, preserved with 2 percent sodium bisulphite (Drum No. 4 - 3/13/53).
- (6) Skipjack viscera, as above (Drum No. 5 - 5/11/53).
- (7) Skipjack viscera, ground, steam-cooked, water added, filtered, and preserved with 2 percent sodium bisulphite (Drum No. 6 - 6/20/53).
- (8) Slipjack viscera, ground, frozen into 5-pound blocks (various dates).

All materials were tested on the captive tunny in the pond, in some cases both before and after sea tests. The responses in the pond were generally weak and variable due to the unresponsive condition of the two surviving tunny during the late winter and spring of 1953. However, all substances did produce a response in at least one out of several tests (Tester et al. 1954).

The extracts in the demijohns and drums were used either as prepared or they were diluted to various strengths on board ship. The frozen material was thawed and extracted with sea water on board ship for at least 1 hour before use.

In addition to the above, two tests were performed with anchovy extract prepared on board by crushing the live bait in buckets of water, allowing the preparation to settle, and then decanting the supernatant liquid.

Methods of Testing

The methods of testing the response of sea fish to the extracts were many and varied. In some cases the extract was poured from buckets from the side or stern of the ship as it described an arc or circle near or around a flock of birds and, presumably, a school of tuna. In the majority of the tests, the tuna school was attracted to the stern with live bait, chumming was stopped, and the extract was poured over the stern into the group of feeding fish. In others, when chumming ceased, the extract was poured in varied quantities and dilutions from the port and/or starboard sides forward of amidships. In still others, it was pumped in a stream or spray from amidships; the pump was controlled from the flying bridge where the fish could be seen.

Results

In all, 16 tests were performed with skipjack or yellowfin extract and 2 with anchovy extract, with several trials per test in some cases. The tests were performed mostly on schools of skipjack or on mixed schools of skipjack and yellowfin, skipjack and tunny, or skipjack and frigate mackerel. In addition two tests were conducted on a pure school of frigate mackerel and one on a school of dolphin.

The results were either negative or inconclusive. Unchummed schools could not be raised by an arc or circle of extract. Chummed schools could not be held at the stern by introducing the extract in small quantities by either bucket or pump.

In a few tests, on pouring in a large quantity of extract after the school had been chummed to the stern and chumming was stopped, a few fish were seen jumping in or passing through the material. It could not be determined whether they were responding to the extract or were chasing stray baitfish. The latter seems to be the more likely explanation.

Discussion

In view of the results outlined above, and others to be reported below in which extracts were used in combination with edible lures, it may be concluded with reasonable certainty that the local skipjack will not respond to extracts of skipjack viscera, yellowfin flesh, and anchovy. It seems likely that this conclusion also applies to local tunny and yellowfin, which showed a response in the pond but not at sea. However, the sea tests on tunny and yellowfin were few in number and were conducted on schools in which they were mixed with skipjack. There is the possibility that they might respond to the extracts if schooled alone.

No sea tests were conducted with extracts of squid and shrimp, both of which might be considered to be a more natural food than skipjack, yellowfin, or anchovy, and therefore might be expected to elicit a response even though the other materials failed. There were several reasons for not using extracts of squid and shrimp, including the lesser availability and higher cost of these materials. The chief reason was that the pond fish had responded well to tuna flesh extracts even though they had been fed exclusively on squid for a period of 2 months. This indicated that they had not been conditioned to any particular food item, but rather were responding to an "attractant" which was generally distributed throughout all food items. It was assumed that this might also be the case with the fish in their natural environment, and that if they responded at all, they would respond (almost) equally well to extracts of tuna, anchovy, shrimp, squid, etc.

The negative results obtained in the sea tests indicate that the sense of smell plays little or no part in the feeding of skipjack, and perhaps other species of tuna as well, in their natural environment. They further indicate that the pond fish had learned to associate the smell of the juices of cut-up food material with the act of feeding and thus exhibited a conditioned response to the extracts, as already discussed in a previous section.

SEA TESTS WITH INEDIBLE LURES

Attention was next directed at a study of the response of tuna at sea to objects which might be visually attractive and which could perhaps be used as chum either alone, with extracts, or with live bait.

Materials

The following materials were prepared and tested (others were prepared, but there was either no opportunity for testing them or it was obvious that no further information would be obtained by testing them):

- (1) aluminum foil: 3/8-inch squares; used dry (floating) or wet with water and Tergitol (slowly sinking).
- (2) tin strips: approximately 1/4 x 2 inches; cut from tin cans (one test) or tin plate (several tests).
- (3) tin triangles: approximately 2 inches across, with concave sides (cut from tin plate from which can tops had been stamped out).
- (4) mica flakes: "artificial snow".
- (5) calcium carbide pellets: approximately 1/4- to 1/2-inch pieces of irregular shape.

Three "drag lure arrays" were prepared and used: (1) an 8-foot iron bar to which were attached small strips of tin with wire leaders; (2) a 10-foot iron bar, V-shaped, to which were attached tin strips, highly polished sport-fishing spoons with hooks, or rubber fish with or without hooks; (3) two 8-foot 1/2-inch pipes connected at one end to a "T" and bent into a V-shape, to which were attached leaders and lures of various kinds. Extracts could be supplied to this last array through a 1/2-inch garden hose (75 feet long) connected to the "T". The extract was dispersed through holes drilled in the arms of the V-shaped pipe.

Methods of Testing

In all tests with inedible objects, the fish were first chummed to the stern with live bait, chumming was stopped, and the materials were thrown to the feeding fish and the response noted. In later experiments a quantitative measure of response was employed: (a) the fish were chummed to the stern, a few were caught by the fishermen, and chumming was stopped although the fishermen continued fishing--the time (in seconds) from the cessation of chumming to the disappearance of the fish was recorded, as well as the number of fish caught during this period; (b) the school was then re-chummed to the stern with live bait, a few were caught, chumming with live bait was stopped and chumming with the objects was started--again, the time to the disappearance of the fish and the number of fish caught during this period were recorded.

In several experiments extracts were introduced at the same time as the inedible lures were presented to the fish.

The drag lure arrays were towed behind the ship at various distances (up to about 75 feet) both in chasing a school without using chum and also after having chummed a school to the stern. In some experiments extracts were released either from the stern or side of the ship, or in the case of the third drag lure, through the garden hose by siphoning action.

Results

Some 40 experiments were conducted with inedible objects and drag lures, including those with and without the use of extract. Typical results for some of those in which the response was measured are included in table 5.

There was no noticeable response to the strips of red cellophane or the mica flakes. The squares of aluminum foil produced a momentary attraction to the chummed fish, but would not hold them.

The tin strips and triangles, which gyrated and flashed in the water as they sank, were temporarily attractive to the fish. When a school was chummed to the stern with live bait, individual tuna could be momentarily lured from the stern to amidships by chumming with strips or triangles of tin from the latter location. This was repeated on several occasions. However, having investigated the flashing tin, the skipjack would return to the stern to feed on live bait. Of 57 skipjack caught from one school during such experiments, 2 had one strip of tin apiece in the stomach. In some tests, when chumming with live bait was replaced by chumming with tin strips from the stern, the fish remained with the ship for a slightly longer period than when no chum was used, but they followed the strips of tin as they sank and therefore kept beyond the reach of the poles.

The calcium carbide pellets gave off bubbles of acetylene gas when thrown into the water, along with a milky precipitate which streamed behind the pellets as they sank. This visual stimulus seemed to attract the fish and hold them for a short period of time. However, no pellets were found in the stomachs of fish which were caught, and no dead or distressed fish were noted in the fishing area after chumming with this active chemical.

The addition of extracts when chumming with visual lures did not seem to cause any added excitement or attraction.

The lure array, either without or with the addition of extract, did not seem to attract the schools when towed near them. However, it was difficult to keep up with the schools when the array was being towed; usually the schools managed to keep ahead of the ship. As shown by data included in table 5, towing the lure array close to the stern after the fish had been chummed with live bait did not seem to hold them for any additional period of time beyond that of the controls.

Discussion

Obviously little success was achieved in attracting and holding schools of tuna with inedible lures of the types which were used. The observation that the tuna will respond to some extent to shiny objects such as strips of tin, silvery objects such as squares of aluminum foil, and effervescing objects such as wet calcium carbide pellets is of interest and possible value in devising other artificial lures. The results suggest that the sense of vision is of major importance in the feeding of tuna in their natural environment.

SEA TESTS WITH EDIBLE LURES

Materials

The preparation of edible lures, consisting basically of gelatin capsules, macaroni, and agar, has been described in a previous section. There was no opportunity of testing the gelatin capsules at sea. Several tests were performed with the non-motile, edible, macaroni and agar preparations. In addition experiments were performed with dead anchovy, cut-up preserved herring, and strips of skipjack flesh, both without and with the addition of extract.

Methods of Testing

In one series of experiments with macaroni and agar preparations the method of testing was similar to that finally adopted with inedible lures, namely, to establish a control time (to disappearance of fish) and count (of fish caught) after chumming with live bait ceased, and to determine a test time and count while chumming the previously live bait-chummed fish with the edible lure. In a second series of experiments direct chumming of the schools with edible lures was attempted. When possible, this was followed by chumming with live bait to see if the school would respond.

With the other experiments (dead anchovy, herring, etc.) the materials were used as chum in some cases after the tuna had been chummed to the stern with live bait and in others without chumming with live bait.

Results

The results of the first series of experiments with macaroni and agar preparations are included in table 5. On comparing the timing and catch under control and test conditions, there is no indication that the edible lures were attractive to the fish.

The second series of experiments, involving direct chumming with the edible lures, was undertaken following a suggestion that the skipjack might be temporarily conditioned to feeding on live bait and, for that reason, might not feed on the edible lures when they were subsequently presented.

Attempts were made to chum ten different schools with edible lures during October and November 1953 with negative or inconclusive results. While attempting to chum three skipjack schools and one dolphin school with macaroni and agar preparations, fish were caught on the trolling jigs soon after chumming began, but there was no assurance that this was related to the chumming. In all other cases except one, the results were negative. For the most part, the schools were "wild". Of nine tuna schools, one was chummed to the stern of the vessel with difficulty using live bait, two failed to respond to live bait, two disappeared before live bait could be used, and for the remaining four, no live bait was available.

The one exception might be described in more detail. A large school of 17- to 25-pound skipjack was chummed in five different passes with one or a combination of the following edible lures: macaroni cooked in skipjack extract and coated with aluminum, macaroni cooked in skipjack extract but uncoated, macaroni cooked in water and coated with aluminum, agar cooked in skipjack extract and impregnated with aluminum, macaroni cooked in anchovy extract and coated with aluminum, and cubes (3/4-inch) of skipjack flesh. On each pass the skipjack were attracted to the stern and, in all, 67 of them were caught with pole and jig. Live bait was not used; none was available. However, it was suspected that the school of skipjack was feeding on opelu (*Decapterus*) and that each time the vessel approached the school the opelu sought refuge under it, thus attracting the skipjack to within reach of the poles. Opelu were spat up by some of the fish which were caught, and were also found in the stomachs. Moreover, some of the fishermen reported having seen the opelu in the water. None of the stomachs which were examined contained edible lures.

In earlier experiments, after skipjack had been chummed to the stern with anchovy, chumming was stopped, and dead anchovy were thrown to the feeding fish. They exhibited continued feeding activity for a time, but followed the dead fish down as they sank. Attempts to chum skipjack schools with strips of skipjack flesh failed. The strips were cut to include the silvery skin on one side, and were about the same size as the anchovy used as chum.

Table 5.--Time (in seconds) and catch (in numbers of fish) during control and test conditions when testing inedible lures, lure arrays, and edible lures (for explanation see text)

Experiment No.	Lure	Control		Test	
		Time	Catch	Time	Catch
S52	Mica flakes	30	2	30	0
S53	Mica flakes plus extract	18	0	15	0
S54	Tin strips	43	4	75	0
S56	Tin strips	-	-	190	0
S49	Calcium carbide	20	0	60	0
S50	Calcium carbide plus extract	25	0	115	2
S57	Lure array (3) with spoons	20	0	20	0
S58	Lure array (3) with spoons and extract	25	1	30	0
		-	-	35	0
S59	Lure array (3) with rubber fish	45	2	36	0
S60	Macaroni plus extract plus aluminum, plugged with cotton	100	14	110	7
S61	Macaroni plus extract plus aluminum	43	5	40	1
		-	-	43	4
S62	Agar strips plus extract plus aluminum	30	1	30	0
		-	-	45	1

Discussion

Failure to attract and hold the schools of tuna with non-motile edible lures perhaps was to be expected in view of the fact that present fishing methods (for skipjack) depend on the use of live rather than dead bait. However, in view of the success in pond tests, it was hoped that the fish at sea would respond, to some extent at least, to the extract-impregnated lures. This hope was not realized. Possibly some response of interest might be noted if the experiments with direct chumming (without the preliminary use of live bait) were repeated under more favorable circumstances, e.g., during the regular summer fishing season when skipjack schools are plentiful and when they respond well to live bait.

There is the possibility that tuna in other parts of the world, particularly those species which will take dead bait on longline gear, might respond to the macaroni or agar preparations. Dr. W. M. Chapman, Director of Research of the American Tunaboat Association, has informed us (verbally) that in the California fishery yellowfin have responded to plain cooked macaroni on occasion. With fish such as these, a positive and consistent response might be obtained if the extract-impregnated, silver-colored macaroni or agar preparations were used.

SUMMARY AND APPRAISAL OF RESULTS

The main object of this investigation has been to study the response of tuna to chemical and visual stimuli in the hope that the information so gained can be utilized in developing a substitute for live bait.

In the past 2 years numerous experiments have been conducted on the response of captive little tunny to chemical stimuli. A screening of over 100 known chemical compounds ranging from simple inorganic to complex organic materials and including several reputed fish attractants has been undertaken. Apart from an apparent sensing of some of the strong-smelling aromatics and an avoidance of some of the highly-colored dyes, the results have been negative. It seems unlikely that further screening of chemicals will produce any worthwhile information.

It has been found that the captive tunny respond with a vigorous feeding reaction to extracts of "food" substances such as skipjack and other fish (flesh, viscera, blood), squid, and shrimp. The response to these several substances was obtained regardless of which one was being fed to the fish as a subsistence diet. However, there was an indication of a slightly better response to a particular extract when the substance from which it was prepared was being used as food. This observation, together with the fact that the fish were being fed on dead, cut-up materials, suggested that the captive fish may have learned to associate the smell of the juices exuding from the cut-up food with the act of feeding and that the response to extracts was entirely conditioned by the nature of the food. This would presume that the so-called "attractant" in the extracts is a substance (or substances) common to the body juices of fish, squid, shrimp, and other forms. As the captive tunny will not forage for live bait occurring in the pond, but rather must be hand-fed, it is unlikely that further information on the question of conditioning can be obtained from pond experiments.

It was hoped that even if there was a partial conditioning of the pond fish, tuna in their natural environment might be naturally "conditioned" to associate the smell of living injured or uninjured prey with the act of feeding, and that they would therefore respond to the extracts. This hope was not realized. A sufficient number of sea tests on skipjack schools were conducted to warrant the conclusion that the fish showed no appreciable response to extracts of skipjack flesh and viscera, extracts of yellowfin flesh, and extracts of live bait. Unfortunately no tests were conducted on "pure" schools of little tunny (the species tested in the pond) or yellowfin (which are known not only to eat dead bait on longlines but to respond occasionally to chumming with cut bait). Also, no sea tests were conducted with extracts of squid and shrimp, both of which might be considered a more natural food than skipjack or yellowfin flesh. Nevertheless the negative results obtained from such sea tests as have been conducted indicate that the sense of smell plays little part in the feeding of tuna in their natural environment.

A study was made of the response of tuna at sea to a variety of inedible lures which were used as chum, both with and without extract, after the fish had been initially chummed to the stern of the ship with live bait. There was a momentary response to shiny objects such as strips of tin, to silvery objects such as squares of aluminum foil, and to effervescing objects such as calcium carbide pellets. Similarly there was a momentary response to dead baitfish. The addition of extract had no apparent effect. These results indicate that the sense of vision plays a much greater role in feeding than the sense of smell. However, neither these visual lures nor a "drag-lure array" (designed to simulate a school of live bait) towed behind the vessel was successful in holding the fish at the stern.

The captive tunny in the pond were used to test a variety of edible lures in which the qualities of visual attractiveness and palatability were combined. Gelatin capsules, pieces of macaroni, and strips of agar treated with concentrated extract were eaten more frequently than when they were not treated with extract. In some of the edible lures, visual attractiveness was increased by coating or impregnating with aluminum powder. In a series of experiments in which the captive tuna were presented alternately with macaroni pieces and agar strips, both cooked in concentrated extract and made silvery with aluminum, the fish showed a preference for the agar. The preference may have been associated with the texture of the material. It became more pronounced with successive testing, suggesting that a learning process was involved.

Sea tests with these edible lures gave negative or inconclusive results. Unfortunately the tests were made during the autumn, when skipjack schools were both scarce and erratic in their behavior. Several of the schools which failed to respond to the edible lures also failed to respond to live bait. The experiments with the more promising substances (particularly with agar strips impregnated with concentrated extract and aluminum powder) should be repeated during the regular summer skipjack season. If they again fail to attract our local skipjack schools, which are notoriously difficult to chum with live bait, it does not necessarily follow that they will also fail to attract skipjack, yellowfin, or other tuna species elsewhere.

In view of the lack of success in attracting local skipjack schools to the stern of a vessel and holding them there with the many materials and combinations of materials which have been used, we may ask what quality of attraction is missing. The missing quality is probably motion--the rapid motion of a living fish or squid, or the rapid motion of a lure trolled through the water. It may be that motion is a prerequisite to attraction by artificial lures. Other qualities of likely importance are size, shape, appearance, texture, and taste of the lures.

Imparting motion to a small object (say, 2 to 4 inches in length and 1/2 to 1 inch in diameter) is a difficult although not impossible task. One method is to use the energy of a chemical reaction and the principle of jet propulsion. Once a satisfactory "motor" has been devised, other problems concerning buoyancy, shape, speed, nature and direction of movement, and fabrication of a self-propelled lure may be tackled. In fabrication the problem of cost looms large, but may be dismissed pending the development of successful experimental models. The problem of making the lure attractive in appearance, texture, and taste does not seem to offer such formidable difficulties as that of imparting motion.

An investigation of methods of imparting motion to small objects is presently underway. If a promising motile lure can be devised, it will be tested on schools of skipjack at sea.

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APPENDIX

A summary of experiments conducted in tank (T) and pond (P) by Tester (ALT) or Takata (MT), with reaction classified as positive (X to XXX), no response (O), or negative (-), over the period July to September 1953. All experiments, except one, conducted on little tunny.

Exp. No.	Date 1953	Substance and preparation	Tank or pond	Observer	Reaction	Remarks
357	7/1	Skipjack viscera, 250 ml. (50 lb. extracted with water, heated, filtered, and decanted --HTP--6/20/53).	P	ALT/MT	O	No indication of attraction--yellowfin only timed and counted.
358	7/1	Skipjack viscera, 500 ml. (Same as #357).	P	ALT/MT	O	Possibly a slight attraction, but not certain.
359	7/1	Skipjack flesh, 1,000 ml. (250 g. extracted with 2,250 ml. water--whole extract--7/1/53).	P	ALT/MT	XX	Speeding and feeding; jacks also reacted.
360	7/1	Skipjack flesh, 1,250 ml. (Same as #359).	P	ALT/MT	XXX	Very good reaction.
361	7/2	Skipjack flesh, 500 ml. stock extract. (equivalent to about 50 g. flesh).	P	ALT/MT	X	Mostly speeding.
362	7/2	Skipjack viscera, 500 ml. (Same as #357).	P	ALT/MT	X	Slight speeding and slight feeding.
363	7/2	Skipjack viscera, 500 ml. (Same as #357).	P	ALT/MT	O	No noticeable reaction.
364	7/2	Skipjack flesh, 1,000 ml. stock extract. (equivalent to about 100 g. flesh).	P	ALT/MT	X	Slight speeding and turning back; yellowfin also reacted slightly.
365	7/2	Anisic aldehyde C. P., 8 ml.	P	ALT/MT	O	Slight speeding in 1st and 2nd periods, but whether or not it was due to material is uncertain.
366	7/6	Skipjack flesh (100 g. extracted with 3 liters water for 3 hours--whole extract).	P	ALT/MT	X	Mostly speeding with little feeding.
367	7/6	Skipjack flesh, 1 liter stock extract.	P	ALT/MT	O	Possibly a slight reaction in 1st period, but not certain--pump turned off except for introducing material.

Exp. No.	Date 1953	Substance and preparation	Tank or pond	Observer	Reaction	Remarks
368	7/6	Skipjack viscera (100 g. extracted with 3 liters water--whole extract--7/2/53)	P	ALT/MT	O	Possibly sensing in 1st period, but no noticeable reaction.
369	7/7	Skipjack flesh (265 g. extracted with 4 liters water overnight--filtrate).	P	ALT/MT	X	Slight reaction with speeding; jacks also reacted slightly.
370	7/7	Squid (180 g. extracted with 3 liters water overnight--filtrate).	P	ALT/MT	XX	Speeding and feeding by tunny and yellowfin.
371	7/7	Citral, 10 ml.	P	ALT/MT	O	No indication of sensing.
372	7/7	Amyl cinnamate, 10 ml.	P	ALT/MT	O	
373	7/8	Hammerhead shark flesh (130 g. extracted with 1,500 ml. water overnight--filtrate).	P	MT	O	Jacks reacted slightly in 2nd period.
374	7/8	Shrimp, 1 liter (250 g. extracted with 2 liters water overnight--filtrate).	P	MT	XX	Definite reaction with feeding.
375	7/8	Shrimp, Same as #374	P	MT	XX	Good feeding reaction; yellowfin and jacks also reacted.
376	7/8	Squid, 1,500 ml. (135 g. extracted with 2 liters water overnight--filtrate).	P	MT	X	Mostly speeding; yellowfin reacted with tunny and independently; jacks also reacted slightly.
377	7/9	Dolphin ovary (177 g. extracted with 2,800 ml. water overnight--whole extract).	P	MT	X	Slight reaction with speeding.
378	7/10	Skipjack flesh, 500 ml. stock extract.	T	ALT/MT	XXX	Good reaction with speeding, turning, and feeding.
379	7/10	Skipjack flesh, 1 liter stock extract.	P	ALT/MT	X	Speeding with some feeding.
380	7/10	Squid, 500 ml. (135 g. extracted with 2 liters water--filtrate--7/7/53).	T	ALT/MT	XXX	Violent reaction, much more so than #378; there was much splashing and feeding.
381	7/10	Squid (100 g. extracted with 1,500 ml. water--filtrate--7/7/53).	P	ALT/MT	X	Much speeding, little feeding, and little turning.

Exp. No.	Date 1953	Substance and preparation	Tank or pond	Observer	Reaction	Remarks
382	7/10	Shrimp (50 g. extracted with 500 ml. water--centrifuged immediately--centrifugate cloudy).	T	ALT/MT	X	Sensing and speeding.
383	7/13	Skipjack blood (130 ml. diluted to 1,000 ml. with salt water--7/10/53).	P	ALT	X	Mostly sensing and speeding but with some returning and swirling; yellowfin reacted with tunny.
384	7/14	Anchovy, 1,000 ml. (120 g. extracted with 1,500 ml. water overnight--whole extract).	P	ALT	X	Very slight but positive reaction; yellowfin and jacks also reacted slightly.
385	7/14	Anchovy, 500 ml. (Same as #384).	T	ALT	X	Slight reaction only at beginning.
386	7/14	Shrimp (50 g. extracted with 900 ml. water filtrate).	T	ALT	X	Slight excitement with feeding reaction.
387	7/14	Plankton (35 g. extracted with 600 ml. water--plankton was collected outside Kaneohe Bay).	P	ALT	X	Sensing with some swirling and turning back.
388	7/14	Squid (67 g. extracted with 1,000 ml. water overnight--whole extract).	P	ALT	XXX	Great excitement, feeding and turning back.
389	7/14	Skipjack flesh, 500 ml. stock extract 7/9/53.	T	ALT	XX	Good reaction with swirling and feeding.
390	7/15	Methionine, 0.5 g.	P	ALT	O	Fish remained deep.
391	7/15	Skipjack flesh, 1,000 ml. stock extract--7/9/53.	P	ALT	XX	Speeding, surfacing; some returning, but no feeding; yellowfin reacted with tunny and also independently.
392	7/15	Hammerhead shark flesh (90 g. extracted with 500 ml. water--whole extract--7/13/53).	T	ALT	O	Slight speeding when they sensed the material but no reaction thereafter; no timing.
393	7/16	Hammerhead shark flesh (150 g. extracted with water--filtrate--7/15/53).	P	ALT	XX	Tunny, yellowfin, and jacks reacted in first 3 periods. This was a good reaction compared with former results obtained with this material.

Exp. No.	Date 1953	Substance and preparation	Tank or pond	Observer	Reaction	Remarks
394	7/16	Skipjack flesh, 1,000 ml. stock extract--7/9/53.	P	ALT	X	Tunny and yellowfin reacted slightly.
395	7/16	Eucalyptol--U.S.P., 6 ml.	P	ALT	O	
396	7/16	Anchovy (100 g. extracted with 1,000 ml. water--whole extract--7/13/53).	P	ALT	O	Practically no reaction; could the eucalyptol tested just prior to this test be responsible?
397	7/16	Squid (100 g. extracted with 1,000 ml. water--whole extract--7/13/53).	P	ALT	X	Weak reaction by tunny and yellowfin
398	7/21	Squid (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	ALT	X	Tunny and yellowfin acted together and independently; fish were still excited and milling after the test.
399	7/21	Skipjack flesh (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	ALT	XX	Better reaction than #398; yellowfin reacted in 9th period.
400	7/21	Shrimp (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	ALT	X	Very slight reaction by tunny and jacks at first, but it didn't last.
401	7/21	Blend of squid, skipjack, and shrimp (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	ALT	XXX	Excellent reaction by tunny, yellowfin, and jacks in first 5 periods.
402	7/22	Skipjack flesh (100 g. extracted with 2,000 ml. water overnight--whole extract--material smelt bad).	P	ALT	XX	Tunny reacted immediately and yellowfin later; no feeding observed but turning, swirling and speeding for both.
403	7/22	Shrimp (100 g. extracted with 2,000 ml. water overnight--whole extract)--smelly?	P	ALT	X	Sensing by tunny in 1st period; slight excitement by yellowfin which didn't last.
404	7/22	Squid (100 g. extracted with 2,000 ml. water overnight--whole extract)--smelly.	P	ALT	X	Definite speeding with some attraction for both tunny and yellowfin.

Exp. No.	Date 1953	Substance and preparation	Tank or pond	Observer	Reaction	Remarks
405	7/22	Blend of squid, skipjack, and shrimp (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	ALT	XXX	Strong reaction with great excitement and swirling; yellowfin reacted slowly.
406	7/23	Blend of squid, skipjack and shrimp (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	ALT	XX	Very good initial reaction by both tunny and yellowfin.
407	7/23	Squid (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	ALT	X	Slight reaction by tunny and yellowfin.
408	7/23	Skipjack flesh (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	ALT	XXX	Excellent reaction with swirling, returning and feeding; yellowfin and jacks reacted with tunny in 7th period.
409	7/23	Shrimp (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	ALT	O	Practically no excitement--a slight swerving only at first.
410	7/27	Isoeugenol, 10 ml.	P	MT	O	
411	7/27	Magna spice concentrated bologna flavor, 10 ml.	P	MT	O	
412	7/27	Blend of squid, skipjack and shrimp (1,000 ml. stock solution--100 g. equiv. with 2% sodium bisulphite--kept at room temperature).	P	MT	XX	Speeding with some feeding by both tunny and yellowfin.
413	7/27	Imitation butter flavor, alcohol soluble, 10 ml.	P	MT	O	Slight repellent effect in 1st period? Slight feeding by tunny and yellowfin on what seemed to be oil in material which floated on surface.
414	7/28	Shrimp (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	ALT/MT	X	Slight reaction with circling and returning.
415	7/28	Squid (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	ALT/MT	XX	Definite reaction in 1st and 2nd periods by tunny and yellowfin with slight speeding.

Exp. No.	Date 1953	Substance and preparation	Tank or pond	Observer	Reaction	Remarks
416	7/28	Skipjack flesh (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	MT	XX	Both tunny and yellowfin reacted in first 3 periods, but no noticeable reaction thereafter.
417	7/28	Blend of squid, skipjack, and shrimp (100 g. extracted with 2,000 ml. water overnight--whole extract--added 2% sodium bisulphite).	P	MT	X	Erratic behavior.
418	7/29	Blend of squid, skipjack, and shrimp (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	MT	X	Slight reaction with turning and speeding; yellowfin sensed material but did not react; jacks reacted in 1st period.
419	7/29	Skipjack flesh (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	MT	XX	Good reaction with turning, swirling, dashing, surfacing and feeding; one yellowfin reacted slightly.
420	7/29	Shrimp (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	MT	X	Weak but definite reaction with slight feeding in 1st period only.
421	7/29	Squid (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	MT	X	Slow reaction--no noticeable speeding; good reaction with feeding by yellowfin.
422	7/30	Squid (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	MT	O	Slight sensing and slight speeding in 2nd period only.
423	7/30	Skipjack flesh (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	MT	X	Weak reaction with some feeding, turning, and speeding; yellowfin sensed material but did not react.
424	7/30	Shrimp (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	MT	X	Slight reaction with some turning and speeding 1st period only.

Exp. No.	Date 1953	Substance and preparation	Tank or pond	Observer	Reaction	Remarks
425	7/30	Blend of squid, skipjack and shrimp (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	MT	XX	Good reaction with turning, surfacing and feeding; yellowfin and jacks sensed material but did not react.
426	7/31	D L Asparagine, 2 g.	P	MT	O	
427	7/31	Anethol, 5 ml.	P	MT	O	
428	7/31	L Arginine monohydrochloride, 2 g.	P	MT	O	
429	7/31	D L Serine, 3 g.	P	MT	O	
430	7/31	D L Leucine, 2 g.	P	MT	O	
431	8/3	Alpha keto glutaric acid, 3 g.	P	MT	O	
432	8/3	D L Histidine monohydrochloride, 2 g.	P	MT	O	
433	8/3	L Hydroxyproline, 1 g.	P	MT	O	
434	8/3	L Tryptophane, 1 g.	P	MT	O	
435	8/3	Guanine, 2 g.	P	MT	O	
436	8/4	Shrimp (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	MT	X	Weak reaction with some returning but no feeding.
437	8/4	Squid (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	MT	XX	Good reaction with returning, surfacing and feeding in 1st period only; sensing but no reaction by jacks.
438	8/4	Skipjack flesh (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	MT	XX	Reaction in 1st period only, but speeding through 5th period; slight speeding by yellowfin.
439	8/4	Blend of squid, skipjack, and shrimp (100 g. extracted with 2,000 ml. water overnight--whole extract)--smelt bad.	P	MT	X	Very weak reaction in 1st period only.
440	8/5	Blend of squid, skipjack, and shrimp (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	MT	XXX	Very good reaction with turning, surfacing, and feeding initially but did not last.

Exp. No.	Date 1953	Substance and preparation	Tank or pond	Observer	Reaction	Remarks
441	8/5	Skipjack flesh (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	MT	XX	Good reaction in 1st period only.
442	8/5	Shrimp (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	MT	X	Slight reaction with some feeding by 2 tunny early in 1st period.
443	8/5	Squid (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	MT	X	Slight reaction in 1st period only; fish confined most of their activities to shallow water.
444	8/6	Squid (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	ALT/MT	X	Speeding and returning but no feeding.
445	8/6	Skipjack flesh (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	ALT/MT	X	Slight reaction in 2nd period and slight feeding in 3rd period.
446	8/6	Shrimp (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	ALT/MT	O	Slight sensing in 1st period only.
447	8/6	Blend of squid, skipjack, and shrimp (100 g. extracted with 2,000 ml. water overnight--whole extract).	P	ALT/MT	O	No noticeable reaction at any time--merely a slight speeding.
448	8/7	Histidine (free base), 2 g.	P	MT	O	Fish swimming deep.
449	8/7	Sodium bisulphite, 2 g.	P	MT	O	
450	8/7	D L Alpha alanine, 2 g.	P	MT	O	
451	8/7	L Lysine monohydrochloride, 2 g.	P	MT	O	
452	8/7	D L Glutamic acid monohydrate, 1 g.	P	MT	O	
453	8/7	L Aspartic acid, 2 g.	P	MT	O	
454	8/10	Glycyl-glycine, 1 g.	P	MT	O	
455	8/10	Alpha amino n butyric acid, 2 g.	P	MT	O	
456	8/10	D L Norvaline, 1 g.	P	MT	O	Most of the tunny did not come within the influence of the material during the early periods.
457	8/10	Xanthophyll oil, 10 ml.	P	MT	O	

Exp. No.	Date 1953	Substance and preparation	Tank or pond	Observer	Reaction	Remarks
458	8/10	D L Tryptophane, 1 g.	P	MT	O	
459	8/10	Chlorophyll, 2 g.	P	MT	-	Repellent effect, especially during first 2 periods.
460	8/11	D L Threonine (with allothreonine), 2 g.	P	MT	O	
461	8/11	D L Threonine, 1 g.	P	MT	O	
462	8/11	Pyridoxine hydrochloride, 1 g.	P	MT	O	
463	8/11	D L Aspartic acid, 2 g.	P	MT	O	
464	8/11	Guanine hydrochloride, 1 g.	P	MT	O	
465	8/11	Uramil, 2 g.	P	MT	O	
466	8/12	D L Lysine monohydrochloride, 2 g.	P	MT	O	Tunny remained at south end of pond for the first 5 periods.
467	8/12	L Proline, 1 g.	P	MT	O	
468	8/12	D L Ornithine monohydrochloride, 1 g.	P	MT	O	
469	8/14	Skipjack flesh (100 g. pale flesh extracted with 2,000 ml. water overnight--whole extract)	P	MT	O	No noticeable response.
470	8/14	Skipjack flesh (100 g. dark flesh extracted with 2,000 ml. water overnight--whole extract)	P	MT	XX	Good reaction with speeding.
471	8/17	Skipjack flesh (100 g. extracted with 2,000 ml. water--whole extract--8/14/53).	P	MT	X	Very slight reaction.
472	8/18	Skipjack flesh (100 g. dark flesh extracted with 2,000 ml. water overnight--whole extract)	P	MT	X	Mostly speeding which lasted through the 5th period; violent reaction and feeding by <u>Abudefduf</u> .
473	8/18	Skipjack flesh (100 g. pale flesh extracted with 2,000 ml. water overnight--whole extract)	P	MT	XX	Good reaction with much speeding and little feeding.
474	8/18	Betaine, 5 g.	P	MT	O	

Exp. No.	Date 1953	Substance and preparation	Tank or pond	Observer	Reaction	Remarks
475	8/18	Skipjack flesh, 100 g. equiv. (600 g. extracted with 2,100 ml. 95% ethyl alcohol and centrifuged; residue extracted again with 1,000 ml. alcohol; centrifugate evaporated to a viscous mass by heating; and concentrate redissolved in water).	P	MT	X	Some turning back and much speeding--speeding lasted throughout experiment.
476	8/18	Skipjack flesh, 200 g. equiv. (same as #475).	P	MT	O	Very slight speeding up.
477	8/19	Skipjack flesh, 100 g. equiv. (same as #475)	P	MT	O	Slight sensing in 1st period only.
478	8/19	Skipjack flesh (100 g. pale flesh extracted with 2,000 ml. water overnight--whole extract).	P	MT	X	Slow reaction--no speeding.
479	8/19	Skipjack flesh, 200 g. equiv. (same as #475)	P	MT	O	No noticeable reaction.
480	8/19	Skipjack flesh (100 g. dark flesh extracted with 2,000 ml. water overnight--whole extract)	P	MT	XX	Good reaction with some feeding.
481	8/20	Skipjack flesh (residue from exp. #475 extracted with water--centrifugate).	P	MT	O	
482	8/21	Skipjack flesh (100 g. dark flesh extracted with 2,000 ml. water overnight--whole extract).	P	MT	X	Slight reaction with some turning and speeding.
483	8/21	Skipjack flesh, 200 g. equiv. (400 g. extracted overnight with 95% ethyl alcohol--centrifugate).	P	MT	O	Possibly slight repellent effect.
484	8/21	Skipjack flesh (100 g. pale flesh extracted with 2,000 ml. water overnight--whole extract)	P	MT	X	Some turning and feeding; this reaction was slightly stronger than that obtained with the dark flesh tested previously (#482).

Exp. No.	Date 1953	Substance and preparation	Tank or pond	Observer	Reaction	Remarks
485	8/21	Skipjack flesh, 200 g. equiv. (400 g. extracted overnight with 95% ethyl alcohol, centrifugate evaporated by heating to viscous mass, and concentrate redissolved in water).	P	MT	X	Turning and speeding--speeding lasted throughout experiment.
486	8/21	Skipjack flesh (200 g. extracted overnight with 2,000 ml. water--whole extract).	P	MT	X	Turning and speeding.
487	8/24	Skipjack flesh (200 g. extracted with 400 ml. water--centrifugate--8/21/53).	P	MT	X	Slight reaction, but much speeding.
488	8/24	Skipjack flesh (200 g. extracted with 200 ml. water and 200 ml. 95% ethyl alcohol--centrifugate--8/21/53).	P	MT	O	Slight speeding in 1st period only.
489	8/24	Skipjack flesh (200 g. extracted with 400 ml. 95% ethyl alcohol--centrifugate--8/21/53)	P	MT	O	Slight speeding in first 2 periods but no noticeable reaction.
490	9/1	D L Tyrosine, 2 g.	P	MT	O	
491	9/2	Phenylalanine, 0.5 g.	P	MT	O	
492	9/2	Thiamine hydrochloride, 2 g.	P	MT	O	
493	9/2	Calcium pantothenate (dextro-rotatory), 1 g.	P	MT	O	
494	9/3	Uracil, 1 g.	P	MT	O	
495	9/3	Creatinine, 2 g.	P	MT	O	
496	9/4	Cholic acid, 2 g.	P	MT	O	Erratic behavior.
497	9/4	Liver fraction "L", 2 g.	P	MT	O	Material dark brown in color.
498	9/4	Musk ketone, 2 g.	P	MT	O	Sped just after passing through material in 1st period--sensing (?).
499	9/4	Liver extract concentrate 1:20, 2 g.	P	MT	O	Material dark brown in color, but fish did not seem to notice it.
500	9/8	Cadaverine dihydrochloride, 0.5 ml.	P	MT	O	
501	9/8	Testosterone U.S.P., 0.5 g.	P	MT	O	

Exp. No.	Date 1953	Substance and preparation	Tank or pond	Observer	Reaction	Remarks
502	9/8	Skipjack flesh, 500 ml. (4,500 g. extracted with 22,500 ml. water in reefer--supernatant--9/2/53).	P	MT	XX	Good reaction in 1st period with turning and speeding--speeding lasted through 8th period.
503	9/8	Musk ambrette, 2 g.	P	MT	0	Reacting to floating leaves; tunny followed leaves as they were blown out of area.
504	9/8	Musk xylol, 2 g.	P	MT	0	
505	9/11	Amyl caproate, 4 ml.	P	MT	0	Fish sped through area on one pass for no apparent reason, but no noticeable reaction to material.
506	9/11	Ionone C - 1, 5 ml.	P	MT	0	
507	9/11	Vioosterol (irradiated ergosterol), 10 ml.	P	MT	0	
508	9/11	Alpha methyl ionone, 5 ml.	P	MT	0	
509	9/11	Phenyl ethyl alcohol, 5 ml.	P	MT	0	
510	9/17	Riboflavin--5--phosphate diethanolamine 2 g.	P	MT	-	Definite repellent effect from this dark orange material.
511	9/17	Tonquin musk synth., 1 g.	P	MT	0	
512	9/17	Casein (nutritional Biochemicals Corp.) 5 g.	P	MT	0	
513	9/18	Eucalyptus oil, U.S.P., 70/75, 2 ml.	P	MT	0	
514	9/18	Crystalline Vitamin A (alcohol), 10 mg.	P	MT	0	
515	9/18	"Astrotone" B R, 2 ml.	P	MT	0	
516	9/18	Phenyl ethyl mercaptan, 2 ml.	P	MT	0	
517	9/18	Adenylic acid (muscle), 0.1 g.	P	MT	0	
518	9/18	Hexahydrobenzoic acid, 2 ml.	P	MT	0	
519	9/21	L Glutamic acid hydrochloride, 5 g.	P	MT	0	
520	9/21	Yeast hydrolysate (enzymatic), 5 g.	P	MT	0	

Exp. No.	Date 1953	Substance and preparation	Tank or pond	Observer	Reaction	Remarks
521	9/21	Lactalbumin, 5 g.	P	MT	O	
522	9/21	Casein hydrolysate (enzymatic), 5 g.	P	MT	O	
523	9/21	Blood fibrin, 5 g.	P	MT	O	
524	9/21	Casein (General Biochemicals, Inc.), 5 g.	P	MT	O	
525	9/21	Gluten, 5 g.	P	MT	O	

SOME "SCHIZOPOD" CRUSTACEANS FROM
THE DEEPER WATER OFF CALIFORNIA

(Plate 1, Text Figures 1-7, Chart 1, Tables 1-4)

BY

ALBERT H. BANNER

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SOME "SCHIZOPOD" CRUSTACEANS FROM THE DEEPER WATER OFF CALIFORNIA¹

By ALBERT H. BANNER²

Two series of collections of Mysidacea and Euphausiacea (here called by their discarded name "schizopoda" for convenience) from the deeper water off California and Lower California (*Baja California*, Mexico) have been made available for this study. The larger collection came from the Hancock Foundation, University of Southern California, Los Angeles. The Foundation had made a series of deep water net hauls off the coast of southern California (with one tow off Lower California) on their vessel, *Velero IV*, and the mysids and euphausids from these tows were loaned me for study through the cooperation of Dr. John S. Garth of that institution (tows listed in Table I). The second series of schizopods, mysids almost exclusively, came from the Hopkins Marine Station of Stanford University. These, also from deeper water, came from plankton tows taken in the Monterey submarine canyon off the coast of central California (tows listed in Table 2); work done under Office of Naval Research contract N6-onr-25127. I was able to examine these specimens through the courtesy of Dr. Donald P. Abbott of that institution.

The mysids and euphausids from the Californian coast are moderately well-known, for previous investigators have reported upon the collections made by the U. S. Fish Commission vessel *Albatross*, upon collections made by the Scripps Institution at La Jolla, and upon various smaller collections. This information for the Mysidacea is summarized in Tattersall (1951), and most of the records of the euphausids are given in either Esterly (1914) or Hansen (1915).

¹Contribution No. 57, Hawaii Marine Laboratory.

²Department of Zoology and Entomology, University of Hawaii, Honolulu 14.

Proof for this paper was read only by the Editor.

TABLE 1
STATIONS OCCUPIED BY THE ALLAN HANCOCK FOUNDATION

Sta. No.	Date	General Locality	Net or Trap Position	Down Time	Fms.	Dir.	Net or Trap Position	Up Time	Fms.	Remarks
1663-43	Dec. 30	4 mi. S of Santa Cruz Island.	33-55-30 119-37-30	1300	430	260°	33-55-00 119-40-30	1400	400	Water haul, deep sea fish, shrimp.
1861-49	July 1	San Pedro Channel.	33-30-30 118-16-42	1228	450		33-25-30 118-14-50	1334		Fish trap towed at 1762 feet.
1863-49	July 9	13.7 mi. ESE of Santa Barbara Island.	33-23-15 118-47-00	1323	710		33-16-50 118-40-32	1520	716	Fish trap towed at 3956 feet.
1864-49	July 10	4 mi. SSW of Church Rock, Santa Catalina Island.	33-14-42 118-21-02	1402	610		33-13-56 118-22-40		630	Fish trap towed at 3277 feet.
1866-49	July 21	San Pedro Channel	33-39-30 118-22-08	1014	420		33-39-01 118-25-12	1110	455	Fish trap towed at 2100 feet.
1867-49	July 21	San Pedro Channel	33-38-27 118-24-45	1147	460		33-37-46 118-22-54	1225	452	Fish trap towed at 1780 feet.
1899-49	Aug. 28	7.0 mi. NE of Bird Rock, Santa Catalina Is.	33-32-47 118-27-50	0952	166	50.5°	33-35-52 118-22-50	1047	166	Ring net towed at 1000 feet.
1900-49	Aug. 28	9.5 mi. NE of Bird Rock, Santa Catalina Is.	33-34-55 118-22-50	1245	333		33-37-42 118-24-50	1425	333	Ring net towed at 2000 feet.
1906-49	Sept. 8	San Pedro Channel	33-29-32 118-20-37	0931	489	015°	33-34-45 118-18-18	1052	300	Ring net towed at 2000 feet, plankton net inserted.
1934-50	Mar. 5	San Pedro Channel	33-32-25 118-24-35	0849	475		33-33-45 118-23-30	1015	485	Dredge. Mud washed thru net.
1991-50	Aug. 23	San Pedro Channel	33-30-24 118-16-54	1135	333		33-26-08 118-14-37	1330	333	Hoop net.
1994-50	Aug. 24	4.5 mi. off Palos Verdes, San Pedro Chan.	33-39-00 118-19-40	1100	300		33-39-06 118-24-58	1240	300	Hoop net.

Sta. No.	Date	General Locality	Net or Trap Position	Down Time	Fms.	Dir.	Net or Trap Position	Up Time	Fms.	Remarks
2008-51	Jan. 31	7.5 mi. SSW of Point Fermin, br 204° T.	33-36-30 118-19-43	1305	(200)		33-36-45 118-23-47	1500	(200)	Plankton net tore loose. Shrimps, fish in webbing.
2009-51	Feb. 15	6 mi. SW of Point Fermin, br 216° T.	33-35-45 118-21-26	1110	450		33-31-10 118-19-38	1340	480	Hoop net touched bottom at 2000 feet.
2037-51	July 7	8 mi. SSW of Point Fermin, br 203° T.	33-35-43 118-20-18	1143	315		33-32-22 118-23-36	1320	315	Hoop net.
2048-51	July 28	San Pedro Channel	33-30-43 118-28-20	1000	456		33-35-43 118-23-28	1210		Hoop net towed at 150 fathoms.
2055-51	Sept. 15	8 mi. SW of Catalina Harbor, br 235° T.	33-25-10 118-41-54	1350	640		33-22-20 118-38-20	1545	560	Net towed at 3181 feet by gauge.
2057-51	Sept. 22	10.5 mi. SSW of W end, Santa Catalina Is., br 201° T.	33-21-34 118-43-50	1150	720		33-18-20 118-35-56	1418	720	Hoop net towed at 2647 feet by gauge.
2060-51	Oct. 18	22 mi. NW x W of N end, Santa Barbara Is., br 285° T.	33-35-00 119-28-04	0845	1030		33-27-33 119-18-22	1150	870	Hoop net towed at 3522 feet by gauge.
2081-51	Nov. 3	12 mi. SSW of Punta Rompiante, Lower Cal, Mex., br 211° T.	27-29-33 115-03-02	0840	630		27-38-14 115-10-00	1114	900	Hoop net towed at 2727 feet by pres- sure gauge.
2084-51	Nov. 18	San Nicolas Basin	33--04-10 119-06-39	1028	970		33-02-26 118-56-57	1345	940	Hoop net towed at 3477 feet by pres- sure gauge.
2135-52	July 23	7 mi. off S coast, Santa Catalina Is.	33-23-35 118-42-12	1042	640		33-14-27 118-34-07	1545	712	Net towed at 3977 feet by gauge.

NOTE: Station 1934-50 is a dredge station and is probably recorded in error; what the correct station might be cannot be ascertained.

However, as the present collections contain some species that have never before been reported from Californian waters and also specimens of various species that permit the reconsideration of some points of taxonomic importance, it was considered desirable to publish the results of the study.

I wish to thank the Allan Hancock Foundation and the Hopkins Marine Laboratory, and Drs. Garth and Abbott, for the privilege of examining the material.

TABLE 2

STATIONS OCCUPIED BY THE HOPKINS MARINE STATION

(All stations were located at $36^{\circ} 42' N.$, $122^{\circ} 02' W.$)

- Tag 27C: Feb. 5, 1951, 1000 m. cable out (no data on greatest depth).
- Tag 36B: March 13, 1951, 1270 m. cable out (no data on greatest depth).
- Tag 44B: April 10, 1951, 1280 m. cable out (no data on greatest depth).
- Tag 82C: Aug. 1, 1951, 455 m. cable out (no data on greatest depth).
- Tag 91B: Aug. 22, 1951, tow to approximately 685 m.
- Tag 121B: Oct. 29, 1951, tow to 995 m.
- Tag 124B: Nov. 6, 1951, tow to 650 m.
- Tag 144B: Dec. 21, 1951, tow to 980 m.
- Tag 147B: Jan. 1, 1952, tow to 790 m.
- Tag 150B: Jan. 8, 1952, tow to 740 m.
- Tag 153B: Jan. 17, 1952, tow to 760 m.
- Tag 159B: Jan. 28, 1952, tow to 860 m.
- Tag 162B: Feb. 4, 1952, tow to 850 m.
- Tag 165B: Feb. 21, 1952, tow to 910 m.
- Tag 168B: Feb. 26, 1952, tow to 780 m.
- Tag 171B: March 5, 1952, tow to 805 m.
- Tag 174B: March 13, 1952, tow to 900 m.
- Tag 177B: March 27, 1952, tow to 1080 m.
- Tag 181B: April 2, 1952, tow to 760 m.
- Tag 184B: April 8, 1952, tow to 960 m.

TABLE 3
CHARACTERISTICS OF FOUR SPECIMENS OF *CHARARASPIDUM ALATUM* (WILLEMOES-SUHM)

Characteristics	Specimens from Hancock Station 2084-51		Specimens from Hancock Station 2081-51	
	45 mm.	28 mm.	40 mm.	21 mm.
Length	Immature female.	Probably an immature female.	Immature female.	Probably an immature male.
Rostral Plate	Anterolateral angles rounded, margins with serrations.	Anterolateral angles rounded, margins smooth.	Anterolateral angles rounded, margins with very few serrations.	Anterolateral angles rounded, margins smooth.
Ocular Papilla	Heavy, with axis parallel to eye.	Same as 45 mm. specimen.	Same as 45 mm. specimen.	Lighter, with axis about 30° divergent to axis of eye.
Antennal squame length/breadth	2.2	2.3	2.3	2.4
lateral teeth	11 pr., regular.	11 pr., regular.	6, 7, irregular.	5 pr., irregular.
Oostegites	Small, lanceolate, reaching to second article of endopod.	None discernible.	Smaller than in 45 mm. female, reaching only to end of basis.	None discernible.
Sternal hooks of thorax	None.	None.	None.	Slightly developed.
Abdominal epimera	1-2, rounded. 3, subacute projection. 4-5, acute tooth. 6, two acute teeth.	1-4, rounded. 5, acute tooth. 6, two acute teeth	1-2, rounded. 3, subacute projection. 4-5, acute tooth. 6, two acute teeth.	1-3, rounded. 4-5, subacute projections. 6, two acute teeth.
Telson lateral spines number, length	5, 6; length equal to half distance between bases.	5 pr.; length almost equal to distance between bases.	5 pr.; length same as 45 mm. female.	5 pr.; length same as 45 mm. female.
terminal spines, length/width of tip of telson	Lateral: 0.51 Medial: 0.46	Lateral: 1.25 Medial: 1.25	Lateral: 1.3 Medial: 1.0	Lateral: 1.2 Medial: 1.0
Outer uropod length	To penultimate lateral spine of telson.	Reaching slightly beyond tip of telson.	Reaching tip of telson.	Reaching tip of telson.
lateral spines	4	3	2	3

MYSIDACEA

Chalaraspidum alatum (Will.-Suhm)

Chalaraspis alata Willemoes-Suhm, 1874, Zeitschr. Wiss. Zool., 24:xx.

Chalaraspis alata Willemoes-Suhm, 1876, R. Soc. London, Proc., 24:592.

Chalaraspis alata G. O. Sars, 1885, Challenger Repts., Zool., 13(37):51, text-figs. 1-2.

Chalaraspidum [alatum] Willemoes-Suhm, 1895, Challenger Repts., Summary, 1:521.

Eclytasps alata Faxon, 1895, Mus. Comp. Zool., Harvard, Mem., 18:219.

Chalaraspidum alatum Tattersall, 1951, U. S. Natl. Mus., Bul., 201:14.

Specimens:

Hancock 2081-51, an immature female 45 mm long, and a 28 mm specimen, probably also a female; 2084-51, an immature female 40 mm long, and a 21 mm specimen, probably a male.

Distribution:

One specimen has been recorded off the coast of California and two specimens off Japan (Tattersall, 1951). Only eight other specimens are known, and all came from the tropical and southern Pacific Ocean, with the exception of the type from the Antarctic, south of Australia (Fage, 1941).

Discussion:

For the change in the generic name from *Chalaraspis* to *Chalaraspidum*, I believe the logic of Tattersall (*loc. cit.*) is correct and should be followed.

The sex of the smaller specimens was determined by the presence or absence of sternal projections on the thorax, structures which Fage (1941, p. 7) showed to be present only in the males.

All four specimens differ from the previously described individuals in that the dorsal carinae of the telson bear numerous (up to 20) short and feeble, articulated spinules. I do not attach any significance to this characteristic because it could have been overlooked easily by the previous

workers. Aside from this, the specimens agree moderately well with the previously published descriptions.

The specimens show some variation one from another. These variations are listed in Table 3. In all of the specimens the anterolateral corners of the rostral plate are rounded. In the smaller specimens the margins of the plate are smooth, but in the larger ones they are serrate. This is probably a growth difference. The variation in the ocular papilla may be a secondary sexual characteristic or it may be a result of growth; it has not been remarked upon before in the literature. The slight differences in the proportions of the squame are likely to be individual variations, as may be those of the armature of its lateral margin and those of the abdominal epimera. The nature of the caudal fan seems to separate the 45 mm. female from the other specimens, for on it the lateral and terminal spines of the telson are short and the telson itself is definitely longer than the uropods. However, with the small number of specimens available, none of which is mature, and with these four specimens showing such variation, it is considered better not to divide the group of specimens into separate species or subspecies.

Tattersall pointed out (*loc. cit.*) that the published descriptions show that there are apparently two types of individuals, those in which the rostral plate has its anterolateral corners produced into acute teeth and whose squame bears only 3 or 4 teeth, and those in which the anterolateral corners of the rostral plate are rounded and which bear numerous teeth on the squame. Of the first type was the female described by Willemoes-Suhm and by Sars, as were the specimens in Tattersall's collection from off Japan. The second type was described on the basis of males by Hansen and Fage, and was represented in Tattersall's collection by an immature specimen from off California. Tattersall suggested that these differences may be sexual; but should future specimens show these not to be sexually dimorphic traits, he recommended a separate species be established for those bearing the rounded corners on the rostral plate.

The subadult females in this collection show that the difference probably is not correlated with sex, so possibly a new species should be described. However, these specimens are not mature and they show variations in other characteristics. Therefore I am of the opinion that the description of a new species is not justified on these few immature specimens, and I further believe it would be better to await with a description based upon such slight differences until far more than 15 mature and immature specimens are known from the world.

Gnathophausia gracilis Willemoes-Suhm

Gnathophausia gracilis Willemoes-Suhm, 1875, Linn. Soc. London, Trans., II, Zool., 1:33.

Gnathophausia dentata Faxon, 1893, Mus. Comp. Zool., Harvard, Bul., 24:217.

Gnathophausia brevispinis Faxon, 1895, Mus. Comp. Zool., Harvard, Mem., 18:216.

Gnathophausia bidentata Illig, 1906, Zool. Anz., 30:229.

Gnathophausia gracilis Tattersall, 1951, U. S. Natl. Mus., Bul., 201:28.

Specimens:

Hancock 2084-51, 2 specimens, immature; 2135-52, 1 specimen, immature.

Distribution:

Fage (1941) gives a chart showing the captures of this species; it is circumtropical but in the Atlantic at least it is found to penetrate into temperate waters. Fage's chart does not show the records cited by Ortmann and Faxon from off the western coast of southern North America. Ortmann (1906) has recorded a single specimen off central California, so the records given above do not extend the known range.

Gnathophausia ingens (Dohrn)

Lophogaster ingens Dohrn, 1870, Zeit. Wiss. Zool., 20:610, pl. 30.

Gnathophausia ingens Sars, 1885, Challenger Repts., Zool., 13 (37):30, pl. 2.

Gnathophausia calcarata Sars, 1885, Challenger Repts., Zool., 13(37):35 pl. 4.

Gnathophausia bengalensis Wood-Mason, 1891, Ann. Mag. Nat. Hist., VI, 8:269.

Gnathophausia doryphora Illig, 1906, Zool. Anz., 30:227.

Gnathophausia ingens Tattersall, 1951, U. S. Natl. Mus., Bul., 201:25.

Specimens:

Hancock 1900-49, 1 specimen; 1994-50, 1 specimen; 2009-51, 4

specimens; 2055-51, 1 specimen; 2081-51, 1 specimen; 2084-51, 6 specimens; 2135-52, 7 specimens.

Hopkins, Tage 144B, 1 specimen; 150B, 1 specimen; 174B, 1 specimen.

Distribution:

This species (as *G. calcarata*) was reported from numerous stations off the coast of northern Mexico and southern and central California by Ortmann (1906) — the northernmost records from the Pacific. The species is well known from the eastern tropical and southern Pacific Ocean, as well as the Indian Ocean and the tropical and subtropical Atlantic Ocean (Fage, 1941).

Discussion:

While the specimen from Tage 150B reaches about 120 mm in length and several from Hancock 2135-52 reach over 100 mm in length, none of the specimens are mature.

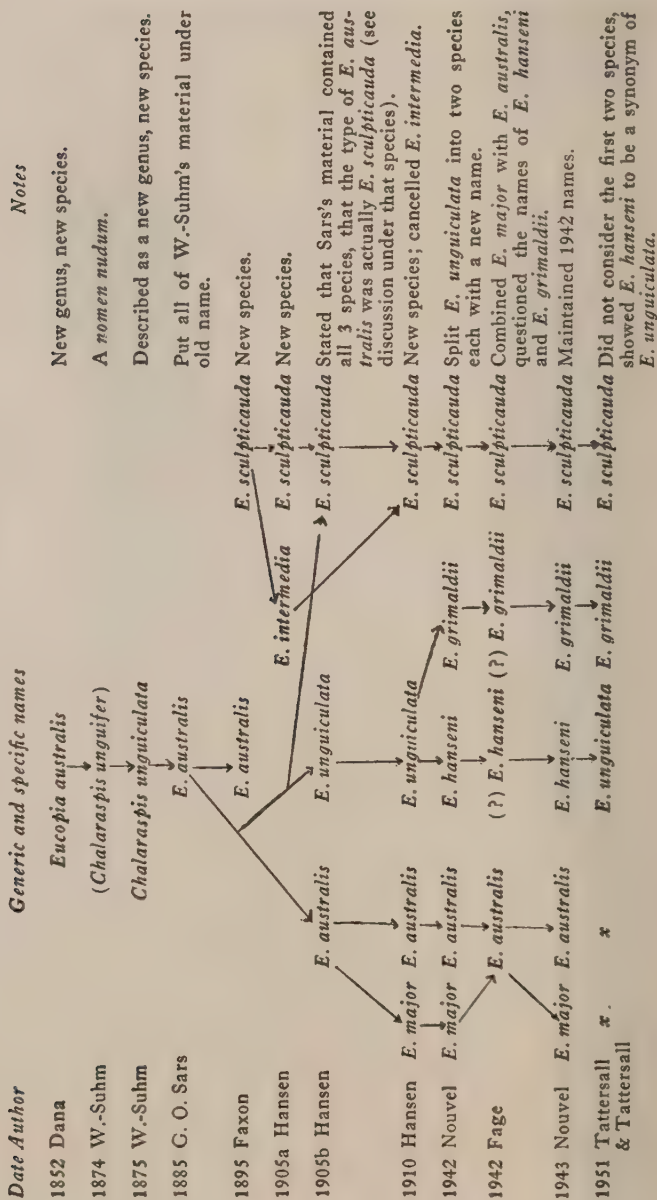
Eucopia Dana

Eucopia Dana, 1852, U. S. Exploring Exped., 13:609.

Chalaraspis Willemoes-Suhm, 1875, Linn. Soc. London, Trans., II, 1:37.

The genus *Eucopia* was established by Dana to accommodate his type species, *E. australis*. From the Challenger material, Willemoes-Suhm (1875) established another genus and species, *Chalaraspis unguiculata*. Sars recognized that Willemoes-Suhm's species was the same as Dana's, and in the Challenger Reports (1885) so stated. In 1893 Faxon described a species differing from *E. australis*, a species he named *E. sculpticauda*. Hansen, in three publications (1905a, 1905b, 1910) described a new species, *E. intermedia*, that he subsequently cancelled as a synonym, and then divided the *E. australis* of Sars into three species, *E. australis*, *E. unguiculata* (a name he reestablished), and *E. major* (a new species). The four existed as the only recognized species of the genus until Nouvel in 1942 (1942a) divided the species *E. unguiculata* (as described by Hansen) into two new species, *E. grimaldii* and *E. hanseni*. In the same year Fage in the Dana Reports stated he believed that *E. major* was a synonym of *E. australis*, and that while he accepted the distinction between *E. grimaldii* and *E. hanseni*, his acceptance of the

CHART 1
Names applied within the genus *Eucopeia*



names was provisional until it could be decided which of the two species should carry the name of the original species. (It should be noted that the type specimen in England was not available to the workers in France during the war.) Nouvel in 1943 rejected both Fage's cancellation of *E. major* and Fage's suggestions about the names of the two species, *E. grimaldii* and *E. hanseni*. Finally in 1951 Tattersall and Tattersall examined the types in the British Museum (Natural History) and reported that the only recognizable specimen left of the Challenger material (upon which Willemoes-Suhm and Hansen had established *E. unguiculata*) was like Nouvel's *E. hanseni* and therefore that name should be put into synonymy and the name *E. grimaldii* be retained. (See accompanying chart.)

In summation, therefore, there are four or five names accepted in this genus: *E. australis* Dana, *E. sculpticauda* Faxon, *E. unguiculata* Willemoes-Suhm, *E. grimaldii* Nouvel and possibly *E. major* Hansen. All of the species except *E. sculpticauda* are accepted as being closely related and are separated by rather slight differences. All will be discussed in the section to follow.

***Eucopia sculpticauda* Faxon**

Eucopia australis G. O. Sars [*pars*], 1885, Challenger Repts., Zool., 13 (37):55 [according to Hansen, 1910, p. 19].

Eucopia sculpticauda Faxon, 1893, Mus. Comp. Zool., Harvard, Bul., 24:218.

Eucopia intermedia Hansen, 1905, Mus. Océanogr. Monaco, Bul., 30:5.

Specimens:

Hancock 2055-51, 2 specimens; 2084-51, 3 specimens; 2135-52, 4 specimens.

Distribution:

This species is primarily circumtropical, with numerous records from the eastern Pacific off Central and South America; from several localities in the central Pacific; and from numerous localities in the western tropical Pacific. Other records are from the Indian Ocean and the Atlantic, from off Iceland to off the Cape of Good Hope (see Fage, 1942). However, in the eastern Pacific it has not been reported north of the Gulf

of Panama (Tattersall, 1951), so the records above constitute an extension of the known range.

Discussion:

The specimens studied were a brilliant coral red even after sixteen months in preservative.

Adults and subadults of this species are easily distinguished by a series of characteristics, like the sculptured telson, the lack of gills on the eighth thoracic legs, the different proportions of the anterior thoracic legs, and the firmer chitin of the exoskeleton. In immature specimens the species is still recognizable, but it lacks the characteristic telson of the adults. The specimens in this collection showed variation in the shape of the telson similar to that noted by Illig (1930).

There is confusion over the name of this species. Unlike Faxon's description of *E. sculpticauda*, which clearly establishes the characteristics of the species, the descriptions of Dana, Willemoes-Suhm, and Sars could be applied to any of the species at present recognized in the genus. Unfortunately the earlier names have priority, so if it can be shown by re-examination of the type specimens that one of these specimens was actually the now accepted *E. sculpticauda*, then this name will have to be put in synonymy. Dana's type for *E. australis* is lost and no neotype has been established. However, the specimens from the Challenger Expedition are still extant, and in 1910 Hansen wrote (p. 19): ". . . I examined the 'Challenger' Schizopoda preserved in the British Museum (Natural History), and I found 4 specimens referred by Sars to *E. australis* Dana. Among these a specimen from Stat. 107 and marked 'male' and 'type' on the label belongs to *E. sculpticauda* Faxon. . . ." If Hansen's determination was correct, and if the designation of the type was that of Willemoes-Suhm for his species *Chalaraspis unguiculata* (now *E. unguiculata*), then this species, until now known as *E. sculpticauda*, should be known as *E. unguiculata*, and the present *E. unguiculata*, if it is to be retained as a species separate from *E. australis*, must be given a new name. If the designation of "type" was that of Sars, I do not believe that any change would have to be made, for it would be a neotype not reported upon in the literature and therefore like a manuscript name.

These conclusions are of course conditional upon the correct identification and interpretation by Hansen. That the identification may be questionable is indicated by Olive B. Tattersall in Tattersall and Tattersall (1951, p. 99): "I have very kindly been given the opportunity of ex-

amining the "Challenger" material in the British Museum. The specimens are in bad condition, but one of them is unquestionably the same species as Nouvel's *E. hanseni* [e.g., *E. unguiculata* (Willemoes-Suhm)] and I am of the opinion that the others are probably the same species. . . . Hansen in 1922 identified the one recognizable specimen of the "Challenger" material as *E. unguiculata*. . . ." If then the "type" and "male" from the Challenger Station 107 is not recognizable, or if it is *E. unguiculata*, then Hansen's remarks in 1910 may be ignored. In this case it would be well to select a type specimen from the Challenger material for *E. unguiculata* and also to select a neotype for Dana's *E. australis*, the latter preferably from the Antarctic Ocean, so future confusion in these names may be avoided.

In any case, I cannot determine the valid name on the basis of material from the North Pacific so I will leave the names as they appear in current usage, with the recommendation that any other worker who is able to examine the Challenger material establish clearly the correct names.

***Eucopia australis* Dana**

Plate 1

Eucopia australis Dana, 1852, U. S. Exploring Exped., 13(10):609; 1855, Atlas, pl. 40, fig. 10a-m.

Chalaraspis unguifer Willemoes-Suhm, 1874, Zeitschr. Wiss. Zool., 24:xx [a *nomen nudum*].

Chalaraspis unguiculata Willemoes-Suhm, 1875, Linn. Soc. London, Trans., II, Zool., 1:40, pl. 8.

Eucopia australis G. O. Sars [? *pars*], 1885, Challenger Repts., Zool., 13(37):55, pls. 9-10.

Eucopia unguiculata Hansen, 1905, Inst. Océanogr. Monaco, Bul., 42:3.

Eucopia australis Hansen, 1905, Inst. Océanogr. Monaco, Bul., 42:6.

Eucopia major Hansen, 1910, Siboga Exped., 37:21, pl. 1, figs. 4a-4b.

Eucopia biunguiculata Leavitt, 1938, Biol. Bul., 74:384 [*lapsus calami*].

Eucopia hanseni Nouvel, 1942, Mus. Océanogr. Monaco, Bul., 818:3.

Specimens:

Hancock 1991-50, 4 specimens; 1994-50, 5 specimens; 2055-51, 2 specimens; 2057-51, about 60 specimens; 2060-51, about 60 specimens; 2081-51, about 100 specimens; 2084-51, about 45 specimens; 2135-52, about 80 specimens.

Hopkins, Tage 150B, 1 immature specimen; 153B, 1 immature specimen; 162B, 3 immature specimens; 177B, 1 immature specimen; 181B, 1 immature specimen; 184B, 1 immature specimen.

Distribution:

This species has been reported under its various names from the deep portions of all oceans from the sub-Arctic to the Antarctic; in the Pacific it has been reported from as far north as the Bering Sea to the Antarctic, south of Australia.

Discussion:

As pointed out in the discussion under the genus, a group of three or four species of the genus *Eucopia* have been accepted as distinct but closely related species. The specimens made available to me by the Hancock Foundation did not seem to fit well within the established species and I felt it was necessary to measure a group of them as accurately as possible on all points previously accepted as being of taxonomic importance in order to determine their relationships.

Unfortunately it is not easy to measure accurately these specimens, for their soft chitin is often broken, twisted and distorted, their soft and broken bodies make them difficult to handle, and finally their complete lack of color in preservative makes the characteristics difficult to discern.

I measured a group of 29 specimens taken from the various tows listed above, including at least two specimens from each of the larger Hancock samples and two from the Tage stations (the others from the Hopkins Laboratory were too immature to be significant). This group of specimens was taken at random from the material available and was not selected to show variation; the only exception to this was that from several of the plankton tows, both larger and smaller specimens were deliberately chosen to determine what effects size and maturity had upon the characteristics.

It is admitted that this group of only 29 specimens is too small to be of great statistical significance, but as they appear to give conclusive evidence on the reliability of some of the criteria used in the separation of the species, and as other specimens more superficially examined did not appear to differ markedly from the range of those measured, this measured sample was deemed to be adequate for the purposes of this study.

In the section below I will give each criterion that has been used to separate the species by the various authors, then the results of this study, and finally any conclusions that I can draw from the results.

Size:

Hansen (1905b, 1910) gave the sizes of his three species as: *E. australis*, 70.5 mm; *E. major*, 40-42 mm; *E. unguiculata*, 27-30 mm, with a maximum of 38 mm. Nouvel (1942a) gave the size of *E. unguiculata* (*E. hansenii* of Nouvel) from the Atlantic as 25-32 mm, with the maximum of 34-36 mm; *E. grimaldii* as 36-38 mm in the eastern Atlantic and 40-43 mm in the western Atlantic. Fage (1942) stated that *E. australis* (in which he included *E. major*) may mature at 42 mm, or be immature at 55 mm; that most *E. unguiculata* were mature from 28-30 mm, but that at times 18 mm and 30 mm females were equally immature; and that in *E. grimaldii* the specimens of 30 mm were mature, but with that species, too, the size at maturity varied. Fage was able to show that these differences in size at maturity were correlated with the nature of the water in which they were found, particularly its temperature and oxygen content.

The specimens here reported range from 13 mm to 40 mm in length, the average being 32 mm. If the four specimens of the 29 less than 25 mm long are excluded, the average length of the specimens is 34 mm. In general those 34 mm long or longer are mature, while those less than 34 mm long are sub-mature or immature.

On the basis of size alone the separation of this species or any species of crustacea is most questionable; however, on the basis of this characteristic, the specimens reported upon are most like *E. unguiculata* and *E. grimaldii*.

Distribution:

Hansen believed that *E. unguiculata* was world-wide in its distribution, that *E. australis* was limited to the Antarctic, and that *E. major* was limited to the tropical Pacific. Fage (1942) showed all species to be world-wide in distribution; that *E. australis* is to be found usually in water more than 1000 m deep where the temperature ranges between 2.1° and 3.9° C. and the salinity ranges between 34.61 and 35.05 parts per thousand, and that *E. grimaldii* and *E. unguiculata* have almost the same depth range as *E. australis*. Tattersall and Tattersall (1951, p. 108) state, "*E. grimaldii* is primarily a bathypelagic form and is most abundant at about 2000 m depth. It can and does penetrate into shallower levels, but has never been taken at less than 300 m. In this respect it differs from *E. unguiculata*, which has been recorded from less than 200 m, though this species also is found most densely at about 2000 m."

The records of these specimens are listed above.

On the basis of distribution, there is no indication that the three or four species may be separate, and there are no clues as to which species these specimens belong.

Frontal plate of the carapace:

Hansen (1910) stated that the frontal plate of *E. unguiculata* was "feebly convex" and that the plates of *E. major* and *E. australis* were "very convex." To render this characteristic into measurable proportions, I measured the distance between median edges of the post-orbital sinuses, and then using that line as a base line, I measured the length of the rostral plate to its anterior tip (Plate 1A). These measurements showed that *E. unguiculata* in Hansen's figure is 4.5 times as broad as long, and

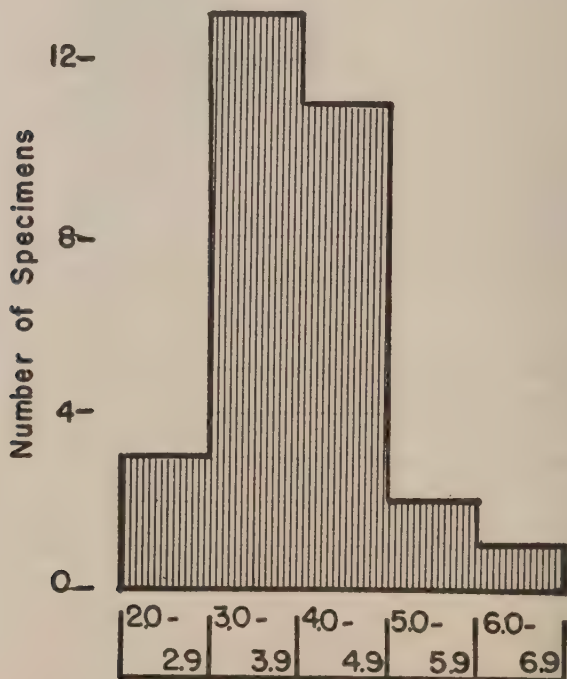


Fig. 1. Length-breadth relationship of the frontal plate of carapace in 29 specimens of *Eucopia australis* Dana. The abscissa represents the breadth divided by the height of the frontal plate (e / d in Pl. 1A).

that *E. major* was 3.0 times. *E. australis*, as shown in Fage's copy of Hansen's 1913a figure (the original paper of Hansen is not available to me) had the ratio of 2.7. Similarly measured, Nouvel's drawings (1942a) showed *E. unguiculata* was 3.8 times as broad as long, *E. grimaldii* 3.3 times and *E. major* 3.0 times. Fage (1942) rejected this characteristic as a valid criterion for the separation of the species because the chitin is soft and too likely to be deformed.

In the measured specimens the rostral projection varies from 2.5 to 6.5 times as broad as long, with most of the specimens varying between 3.0 and 4.0 times as broad as long (Fig. 1). No correlation between body length and convexity is apparent in these specimens.

On the basis of this study it appears that the convexity of the rostral plate must be rejected as a valid criterion for the separation of the species.

Eyes:

It was primarily on the basis of the eyes that Hansen (1910) separated *E. unguiculata* from *E. major* and *E. australis*, stating that in the former, the "eyes look essentially outwards, occupying more than one-third, frequently about two-fifths, of the outer margin of the whole appendage (stalk + cornea)" while in the latter the "eyes look essentially forward, occupying less than one-fourth of the outer margin of the whole appendage." He further stated that *E. major* has "Eye-stalks (with eyes) scarcely twice as long as broad" and *E. australis* has "Eye-stalks (with eyes) more than twice as long as broad." In his figures in the same work the eye in the drawing of *E. unguiculata* was 1.8 times as long as broad, with the cornea occupying almost 0.5 the entire length, while in *E. major* the structure was 1.85 times as long as broad and the cornea occupied one-fourth the length of the entire structure if measured down the center of the stalk (see Plate 1A). *E. australis* (as redrawn from Hansen by Fage) had the eyestalk two times as long as broad with the cornea occupying approximately one-fourth of the outer margin.

In Nouvel's (1942a, 1943) drawings similar measurements showed that *E. unguiculata* had a stalk 2.0 times as long as broad, with the cornea occupying 0.5 of the length; *E. grimaldii* 2.0 times as long as broad with the cornea occupying 0.4 of the length; and two drawings of *E. major* showed the stalk 2.3 and 1.6 times as long as broad, with the corneas occupying 0.23 and 0.27 the total length of the appendage.

Fage (1942) rejected the difference between *E. australis* and *E. major* stating "... la chitine est extrêmement molle . . . et ceci est évident pour les pédoncules oculaires particulièrement déformables."

The variations in the specimens examined is given in Figures 2 and 3a-b. The observed range in the length-breadth ratio lies between 1.5 and 2.8, with most of the specimens showing eyestalks about 2.0 times as long as broad. The cornea was found to vary between 0.20 and 0.45 as long as the entire stalk, with that of most specimens lying between 0.34 and 0.37 times as long as the stalk. There was no apparent correlation between the eye proportions and the size or maturity of the individual. (Note that in Figure 3a the interval of the graph is small to show the spread on the characteristic, while in Figure 3b the ratios are grouped to show an approximation of a normal curve. It is realized that many additional measurements would have to be made to determine accurately the perimeters of the curve).

This set of figures shows that no reliance should be placed on the characteristics of the eyes for the separation of the four species, for approximately half of the specimens have eyes less than twice as long as broad, and half have eyes more than twice as long as broad; one-third of the specimens have corneal lengths of one-fourth the length of the eyestalk, as supposedly characteristic for *E. australis*, and one-third have

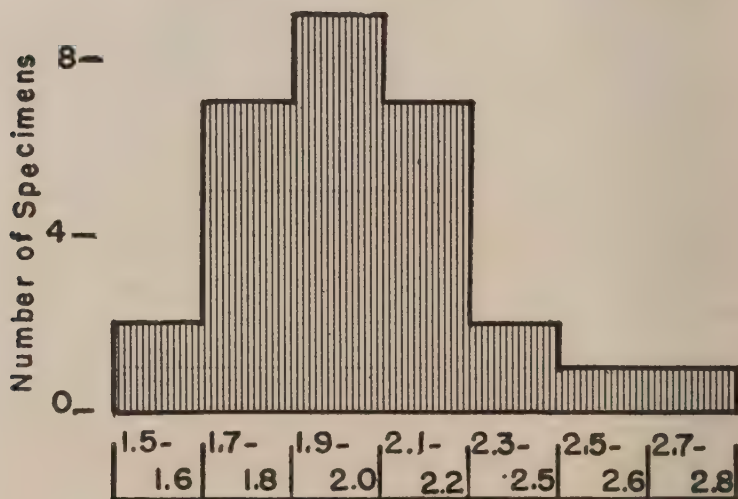


Fig. 2. Length-breadth relationship of the eye in 29 specimens of *Eucopia australis* Dana. The abscissa represents the length of the entire eyestalk divided by its breadth at its maximum diameter (b / c in Pl. 1A).

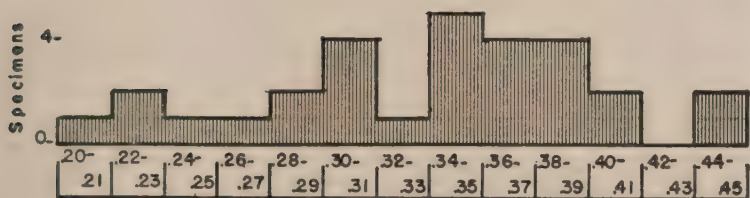
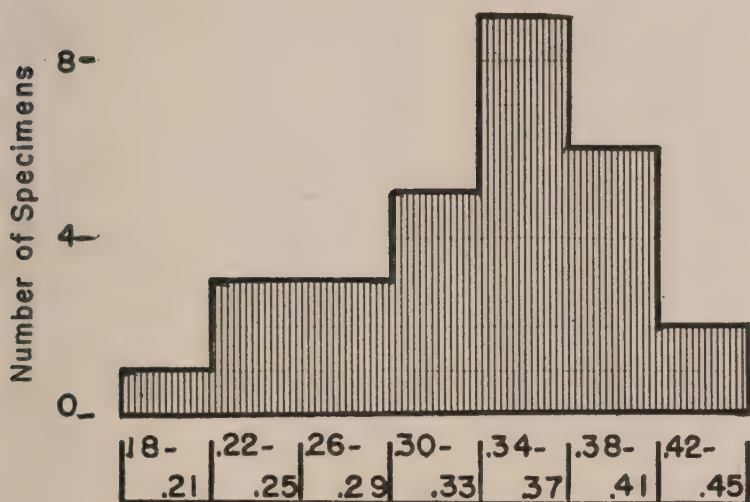


Fig. 3. Cornea length to total length in eyestalk in 29 specimens of *Eucopia australis* Dana. The abscissa represents the length of the cornea, measured along the lateral surface of the eyestalk, divided by the total length of the eyestalk (a / b in Pl. 1A). The upper graph shows the ratios grouped and the lower graph shows the ratios more widely spread to illustrate the almost random scattering obtained with this small group of specimens. Graphs similar to the lower could be drawn for most of the ratios discussed in the text.

corneal lengths of one-third the eyestalk length, as supposedly characteristic for *E. unguiculata* and *E. grimaldii*, and the rest of the specimens lie between these limits.

Antennules:

Nouvel (1942a, 1943) and Fage (1942) pointed out that the terminal article of the antennule would serve to distinguish the species. They stated that in *E. unguiculata* this article is as long as or slightly longer than broad across the distal end and that the internal distal lobe is as long as the median (or external) lobe. In *E. grimaldii* the article is reported to be 1.5 times as long as broad and the internal distal lobe markedly longer than the median lobe. In *E. australis* (*E. major*) the article is 1.5 times as long as broad, with the internal lobe somewhat intermediate in size between those of the other two species. Fage further stated that the

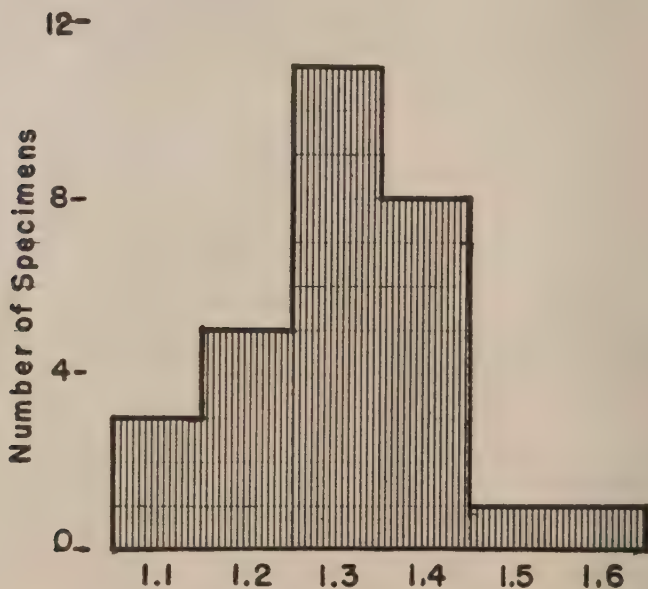


Fig. 4. Length-breadth relationship of the distal article of the antennular peduncle in 29 specimens of *Eucopia australis* Dana. The abscissa represents the length divided by the breadth across the free end of the tip (a/b in Pl. 1B).

proximal articular surface is sinuate in *E. australis* and straight in *E. unguiculata*. (See Plate 1B.)

Most of the specimens examined have proportions between those given for *E. unguiculata* and for *E. australis* and *E. grimaldii*, but a few specimens reach the sizes given for the various species (Fig. 4). However, in none of the specimens does the inner lobe approximate the length reported for *E. grimaldii* and *E. australis*; in most it was approximately equal in length to the outer lobe, and in a few it was slightly longer. The proximal articular surface was difficult to see and almost impossible to measure in most specimens, and as a consequence I did not place much emphasis upon it. However, where observed it was usually straight like in *E. unguiculata*, and in a few it appeared to be very slightly sinuate but not as much so as reported for *E. australis*.

From these specimens, therefore, the differentiation between *E. unguiculata* and *E. grimaldii* based on the length of the inner lobe of the third antennular article may be acceptable; the same distinction between *E. unguiculata* and *E. australis* is questionable. The use of the length-breadth relationship of the article for distinguishing between the species is definitely questionable, and the distinction based upon the articular surface is probably too subtle to be useful.

Antennal Squame:

Nouvel (1942a, 1943) used the distal article of the squame to distinguish between *E. unguiculata* and *E. grimaldii*, stating that the article was more symmetrical about the midline in *E. unguiculata* than in *E. grimaldii*. Fage (1942) pointed out that the article was about 2.0 times as broad as long in *E. australis* while it was less than 2.0 times as broad as long in *E. unguiculata* and *E. grimaldii* (his drawings of *E. unguiculata* show it to be about three times as broad as long). Fage further stated that the lateral margin of the basal portion of the squame was straight in adult females of *E. australis*, while in the males and young of that species, as well as all forms of *E. unguiculata* and *E. grimaldii*, the basal portion was dilated or convex. (See Plate IC.)

In these specimens the tip of the antennal squame varies from less than 2.0 times as broad as long to 3.0 times, with most of the specimens having the ratio of about 2.2 (Fig. 5). In all, the tip is moderately asymmetrical (the proportions were not measured), approaching at times the condition found in *E. grimaldii*. The difference in the outer margin of the basal portion of the squame is in no case as pronounced as that shown by Fage, and varies between being almost straight to showing a slight curve;

the curvature apparently is not correlated with the sex of the specimen.

It does not appear that the characteristic of the antennal squame is adequate for the separation of the species.

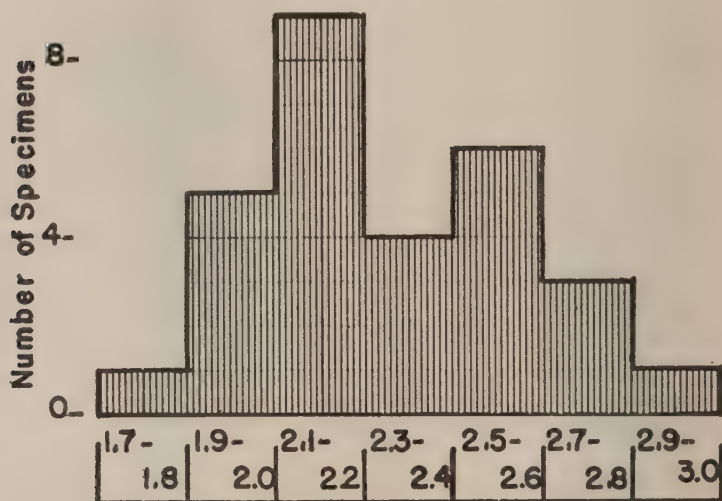


Fig. 5. Breadth-length relationship of the articulated tip of the antennal squame in 29 specimens of *Eucopia australis* Dana. The abscissa represents the breadth of this article divided by its length (a / c in Pl. 1C).

Length of Inner Uropod:

Nouvel stated (1942a, 1943) that the inner uropod is shorter than the telson in *E. unguiculata* but that in *E. australis* and *E. grimaldii* it is longer than the telson, while in *E. major* it is variable. (See Plate ID.)

In the specimens at hand it also varies. Actual measurements were not taken, but for each specimen it was noted whether the uropod was shorter than, equal to, or longer than the telson. In 3 specimens the uropods are longer, in 12 they are approximately equal in length to the telson, and in 12 they are slightly shorter (two specimens had defective uropods).

In view of the reported variation in *E. major*, and in view of the variation in these specimens, it would not appear that this is a valid characteristic for the differentiation of the species.

Outer Uropods:

Hansen (1910) differentiated between the three species as follows: in *E. unguiculata* "terminal joint of the exopod distinctly broader than long"; in *E. australis* "Terminal joint of the exopod of the uropods a little longer than broad." Yet in his figures he showed *E. unguiculata* and *E. major* as having exactly the same length/breadth ratio (a ratio of about 0.93 — see Plate 1D). In Fage's reproduction (1942) of Hansen's 1913a drawing of *E. australis*, the tip was exactly as long as broad. Fage rejected this differentiation with "Quant aux dimensions relatives de l'article terminal des uropodes, on verra qu'elles comportent des variations individuelles souvent en rapport avec l'âge des individus."

Between *E. unguiculata* and *E. grimaldii*, Nouvel (1942a) made a different distinction: in *E. unguiculata* the angle made by the articulation of the tip of the straight outer margin of the basal article is more acute than that of *E. grimaldii*. By actual measurement on his drawing with a protractor, the angle is about 75° in the first species, 80° in the second.

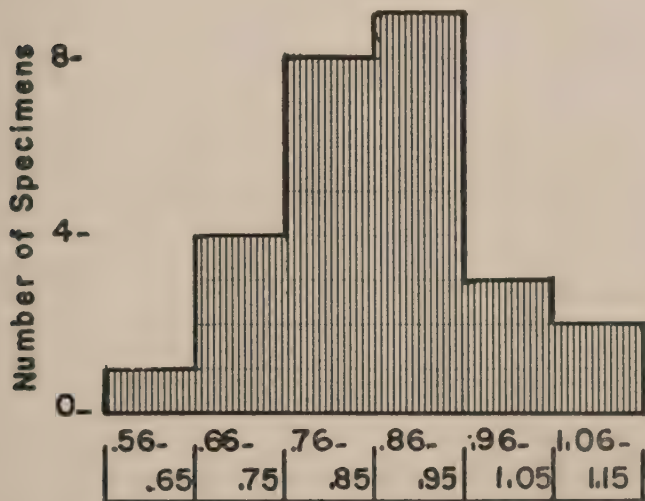


Fig. 6. Length-breadth relationship of the articulated tip of the outer uropod in 27 specimens of *Eucopia australis* Dana. The abscissa represents the ratio obtained by dividing the length of this article by its breadth across the base (b/a in Pl. 1D).

In only four of the series of twenty-seven specimens measured (in two the uropods were broken) the length of the distal article equals or is greater than its breadth; in most, the length of the distal article is between 0.85 and 0.95 its breadth (Fig. 6). The angle made by the articulation was not possible to measure with accuracy with the optical equipment available, but the angle was approximated on the lines of an ocular micrometer and compared visually to a protractor. The angle was estimated thereby to the closest 5° . Seven specimens have the angle of approximately 90° ; 4 specimens, 85° ; 8 specimens each 80° and 75° .

Therefore on the basis of these specimens it may be concluded that the use of the angle of articulation of the tip of the outer uropod is of dubious worth; that the proportions of the uropod tip are probably, but not definitely, without significance for the separation of the species. However, considering also Fage's observations on *E. major* and *E. australis*, it is evident that this criterion, too, should be discarded.

Telson:

Both Nouvel (1942a, 1943) and Fage (1942) have pointed out the differences in the tip of the telson. In all species the distal portion of the telson is armed with a double series of spines, those that are long and somewhat distant from one another and those that are shorter and packed closely between the bases of the longer spines (Plate 1D). According to these authors, in *E. unguiculata* there are about a dozen spines, subequal in length, of the shorter series between the penultimate long spine and the spines at the tip of the telson, with the penultimate spines 5 to 9 times the length of the shorter spines immediately adjacent distally (proportions taken from drawings). In *E. grimaldii* there are usually 2 or 3 shorter spines in the last series, also subequal in length, but the penultimate long spines are only about 3 times the length of the shorter ones. In *E. australis* there are 6-7 spines in the last series, but these are graduated in size, with those located nearer to the tip definitely longer than the more proximal ones; the penultimate long spines are 3 to 5 times as long as the shorter spines immediately adjacent distally.

In the specimens measured (four specimens omitted because of the loss of the telson) the number of shorter spines in the last series range from a minimum of 5 to a maximum of 16, usually asymmetrical, with one side having several more than the other. Most of the specimens have 7 or 8 spines in this series (Figs. 7a-b). In all cases the spines of the last series are subequal in length. The length of the spines is relatively difficult to measure on the specimens, but in 9 the penultimate long spine is about 3

times as long as the spines adjacent; in 7 it is 4 times as long; in 8 it is 5 times as long; and in one it is 6 times as long.

In this series of specimens, then, the number of spines in the final series and the relative length of the penultimate long spines, when compared to the adjacent distal spines, resembles *E. australis*, but the equality of length of the spines resembles *E. unguiculata*. No specimens were found that approach the condition reported for *E. grimaldii*.

This series of specimens is sufficiently uniform to be considered as derived from a single species. While the individuals manifest wide variation, in no case are the individuals definitely set off by any characteristic from the mass of specimens, and moreover the specimens at the extremes of variation of one characteristic are normal on other characteristics, as, for example, the specimen with the shortest cornea is about average in the proportions of the tip of the squame, and the specimen with the most convex frontal plate has corneas occupying 0.3 of the eye stalk.

Even without this study the separation of species which show such a distributional pattern would be rather suspect if it were based upon such subtle characteristics. These species are bathypelagic and are found co-existing in almost all deeper bodies of water. Moreover, they have been shown by Fage to be influenced both in their size and their physical characteristics by the physico-chemical nature of the water that they inhabit. If one species of the complex were limited to the surface waters of the north Atlantic, another to the surface waters of the austral Pacific, and a third to the deeper waters of the tropical Pacific, then greater faith could be placed upon these slight differences.

In spite of the evidence from this study, and in spite of the distributional pattern, I am loathe to lump all four species together, for this sample is from but a small portion of the total range. To be certain about the uniting of the species it would be necessary to study specimens from other parts of the Pacific, from the Indian and from the Atlantic Oceans. Any decision made on the basis of such a restricted sample as this must be tentative.

But as not a single characteristic previously used in the separation of the four species can be shown to be constant, with the exception of the conformation of the third antennular article and the telson, characteristics that can separate only *E. grimaldii*, I am forced to follow Fage in the cancellation of *E. major*, and to place *E. unguiculata* also in

synonymy. Further, I recommend that a series of specimens that are now recognized as *E. grimaldii* be studied in a similar fashion to determine whether that species, too, is merely an extreme of the normal variation or at most a subspecific variant of the species, *E. australis*.

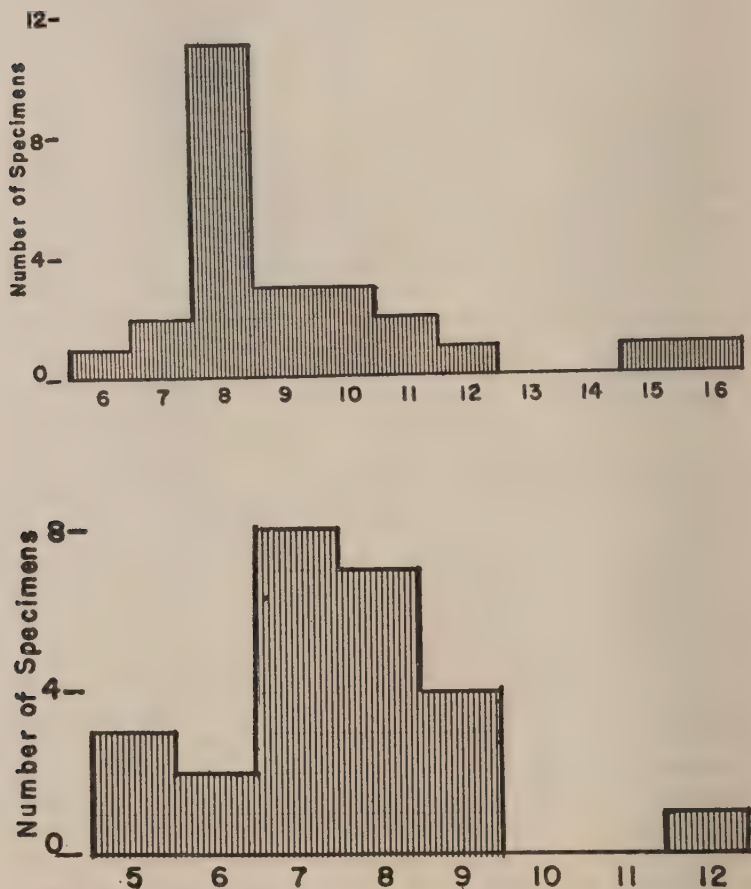


Fig. 7. The maximal and minimal numbers of short spines in the last series on the telson in 25 specimens of *Eucopia australis* Dana. The upper graph represents the maximal number counted on either side of the telson, the lower graph the minimal (the spines counted are those included in the bracket *c* in Pl. 1D).

***Boreomysis californica* Ortmann**

Boreomysis californica Ortmann, 1894, Mus. Comp. Zool. Harvard, Bul., 25:106, figs. 4-14.

Boreomysis media Hansen, 1912, Mus. Comp. Zool. Harvard, Mem., 35:190, pl. 1, figs. 2a-2b.

Boreomysis kincaidi Banner, 1948, R. Canad. Inst., Trans., 26:362, pl. 2, figs. 3a-3j.

Boreomysis californica Banner, 1948, R. Canad. Inst., Trans., 26:367, pl. 4, figs. 5a-5i.

Boreomysis californica Tattersall, 1951, U. S. Natl. Mus., Bul., 201:52, figs. 9-10.

Specimens:

Hancock 1991-50, 2 specimens; 2055-51, 1 specimen; 2057-51, 6 specimens; 2060-51, 9 specimens; 2081-51, 15 specimens; 2084-51, 42 specimens; 2135-52, 10 specimens.

Hopkins, Tague Stations, 27C, 44B, 91B, 121B, 124B, 144B, 147B, 150B, 153B, 159B, 162B, 165B, 168B, 171B, 174B, 177B, 181B, 184B; (aliquot or whole samples examined containing from one to less than 100 specimens).

Distribution:

Various records by previous authors have shown that the species ranges along the Pacific Coast of the Americas from off Peru (Hansen, as *B. media*) to 59° N., off Alaska (Banner); westward it reaches to the Sea of Okhotsk (Tattersall). It has also been reported as *B. media* from the Atlantic and Indian Oceans (Illig, 1930). The present records, therefore, do not extend the range.

Discussion:

Ortmann's original description was very brief and ambiguous. In my 1948 paper I redescribed what I interpreted to be this species from specimens collected off Alaska, and I also described what I thought was a new but related species. In 1951 Tattersall redescribed *B. californica* from the specimens at the U. S. National Museum. However, the two redescriptions of *B. californica* did not agree. The specimens I identified as *B. californica* had laterally expanded corneas, while the ones I described as a new species, *B. kincaidi*, showed narrow hemispherical

corneas. On the other hand Tattersall, evidently not finding the form with the broadened corneas, described the same form as my *B. kincaidi* as *B. californica*.

Fortunately in the series of specimens now available to me I can resolve the difficulty. The only important difference between *B. kincaidi* and *B. californica*, and between my interpretation of *B. californica* and that of Tattersall, is in the breadth of the corneas. There were other differences listed in my paper, but these are slight and within the range of variation of the species. From the present group of specimens, especially from the extensive collections loaned by the Hopkins Marine Laboratory, I measured the eyes of a large number of specimens.

Most of the adults, ranging between 18 and 20 mm in length, have eyes with definitely broadened and dorsoventrally compressed corneas; on these the breadth of the corneas usually is between 0.6 and 0.7 the length of the entire stalk; the corneas are at times irregular, but usually of maximum height anteriorly and more compressed posterolaterally, and usually about 0.7 to 0.8 as high as broad. However, on sub-mature specimens the corneas are less expanded and less compressed; for example, two 15 mm females have corneas 0.5 and 0.6 as broad as the stalk is long, and 0.85 and 0.9 times as high as broad. On specimens less than 10 mm long the corneas are very small, not more than two-thirds as broad as the stalk, and only 0.4 as broad as the stalk is long; their corneas are round when seen in side views. In all size groups the development of the eyes is somewhat variable.

The adults, therefore, lie somewhat between the specimens I had described as *B. kincaidi* and those I had identified as *B. californica*, but the range of variation, especially when the immature specimens are considered, bridges the gap between the two described forms.

Variations in other characteristics were also noted: The rostrum, in most specimens, makes an angle of about 45° to the longitudinal axis of the body, but in some it is almost parallel to this axis. The development of the denticles around the telson cleft also varies somewhat, with those of the anterior portion of the cleft in some of the specimens leaving a slightly wider space between their inwardly directed tips than did those located more posteriorly, a characteristic that is much more highly developed in *B. microps* G. O. Sars. Finally, in many, but not all, of the adult specimens there are several rounded rugae on the anterior portion of the cephalothorax below the base of the rostrum and above and between the bases of the eyes.

It appears that this variation in the eyes removes the chief differentiation between this species and *B. sibogæ* Hansen (1910, p. 25, pl. 2, figs. 3a-3e). There are other differences pointed out by Hansen in his discussion for *B. media*, for example, in the proportions of the telson, but these differences are not great and easily may fall within the range of the normal variation of the species. However, as *B. sibogæ* was found in the western Pacific, far beyond the known range of this species (Illig's *B. media* excepted) it was decided to permit the species to stand until specimens from the western Pacific could be examined.

***Echinomysis distinguenda* Coifmann**

Echinomysis distinguenda Coifmann, 1936, Boll. Zool., Torino, 7:87, fig. 5.

Specimens:

Hancock 2037-51, 1 specimen; 2048-51, 7 specimens; Hopkins, Tage 36B, 1 female, mature.

Distribution:

This species has been known before only from the type specimen that was taken southeast of the Sea of Aden in the Indian Ocean. That these specimens were collected off southern California is not remarkable in view of the extremely great ranges of many species of bathypelagic mysids.

Discussion:

This genus easily can be distinguished from the genus *Cæsaromysis*, which is superficially very similar, by the presence of the well-developed exopodite on the first thoracic legs (maxillipeds), which is reduced to a mere lobe in *Cæsaromysis*, and by the larger antennal squame, especially in the females. However, it is most peculiar that two genera, so similar in almost all features, should be separated by such characteristics. One is led to suspect that perhaps the characteristics are neither fundamental nor important, although no specimens yet reported upon would indicate this.

Two species of the genus *Echinomysis* have been described, *E. chuni* Illig (1905 and redescribed by the same author in 1930), and *E. distinguenda* Coifmann (1936a and redescribed in 1936b). The specimens at hand appear to be of the latter species although they do not agree perfectly with Coifmann's descriptions nor with her criteria for the separation of the two species.

Coifmann lists seven characteristics that would serve to separate the two species. These specimens agree with two of her criteria: First, she states that in her species the rostral projection is rounded and bears five spines around its anterior margin, instead of being pointed and bearing the spines laterally; and, second, in *E. distinguenda* the antennal squame reaches only slightly beyond the end of the second antennular article, instead of near the end of the third article. Two of the criteria listed by Coifmann were found to be variable in these specimens: she stated the limits of the coverage of the body and appendages anteriorly and posteriorly by the carapace, but in these specimens it was found that the carapace not only differs slightly in size, but also can be shifted with ease anteriorly or posteriorly, so that the extent of coverage over the eyestalks or over the posterior thoracic segments depends not upon the animal but upon how it was handled, in the net, in the preservative, and in the examination dish. In one of the criteria discussed by Coifmann these specimens lie intermediate, for she states and shows that her specimen was lacking lateral processes on the abdominal segments, while in *E. chuni* the lateral processes are heavy, extended and acute; in these specimens the lateral processes of the bases of the pleopods are somewhat extended—not as much as those of *E. chuni*—but rounded. In one characteristic these specimens are more like *E. chuni*, for in *E. distinguenda* the eyes are located at abrupt right angles to the straight heavy stalk, while in *E. chuni* the stalk is thinner and curved, like that found in all of these specimens. However, in *E. chuni* the lateral and anterior corneas are shown to be almost meeting, while in these specimens and in the figures of *E. distinguenda* the two sets of corneas are separated by a space equal to more than half the breadth of the lateral cornea. Finally, the last characteristic listed by Coifmann, that of the first pleopods of the mature males, cannot be applied to these specimens for none of the mature specimens are males.

These specimens indicate that there possibly should be one more differentiating characteristic added to the list: *E. chuni* is depicted as having a large number of spines on the terga of the abdominal segments—the second segment, for example, bears 13 spines, while in the figure *E. distinguenda* has about half as many, the second segment bearing only 7. In these specimens the number of spines is also reduced, usually from 5 to 7 on the second segment.

In spite of the variability of some of the characteristics emphasized by Coifmann, and in spite of the fact that the eyes of these specimens in some respects are more like *E. chuni*, I believe that *E. distinguenda* can be accepted as a valid species, distinguished principally by the form of the rostrum and of the antennal squame, and that these specimens belong to that species.

Caesaromysis vancleveii Banner

Caesaromysis vancleveii Banner, 1948, R. Canad. Inst., Trans., 26:389, pls. 7-9, figs. 9a-9v.

Specimens:

Hopkins, Tague Stations, 36B, 82C, 124B, 162B, 174B, 177B, 181B, 184B; 16 specimens in all.

Distribution:

This species has been known previously only from the deeper waters from off Oregon to Alaska. It is interesting to note that this northern species coexists with *Echinomysis distinguenda* at the latitude of Monterey Bay (36° 42' N), and there it is by far the more common of the two, while in the Hancock material *E. distinguenda* is not uncommon, but *C. vancleveii* does not appear at all.

Discussion:

Unfortunately in this whole series there are only two mature individuals, a male from Station 124B and a female from 177B. These two specimens agree only moderately well with the specimens from further north, differing principally in the relative lengths of the uropods, with the outer only slightly longer than the inner, and with the antennal squame of the male bearing only 4 instead of 9 setae. In other characteristics established for the separation of *C. vancleveii* from *C. inispida* Ortmann, like the greater number of spines on the body and the circlet of setae around the distal end of the basis of the second thoracic leg of the female, the specimens agree with *C. vancleveii*.

The smaller specimens are much more difficult to assign to species. Most of them are so immature that in the females the oostegites are simple lobes on the bases of the posterior legs, and in the males the *process masculinus* is hardly visible. In these specimens variation was observed in every characteristic that could separate the two species. In the males the squame of the antenna is poorly developed and often with only one or two setae; in the females the second antennular article is relatively

shorter, and they are lacking the circlet of setæ around the basis of the second thoracic legs; in both the relative lengths of the uropods are variable, with the inner uropods equal to or, in one specimen, longer than the outer. However, in all specimens, while the number of spines on the carapace and on the abdominal terga of the males is less than in mature forms, it is greater than the number reported for *C. hispida*.

On the basis of this collection, I suspect that *C. vanclevei* may be a synonym of *C. hispida* and that these specimens represent part of an intergradation that will be found to be more complete when more specimens are studied from other areas. However, as the two adults clearly could be separated from *C. hispida*, I will maintain the separation of *C. vanclevei* until more intergrading specimens are examined.

EUPHAUSIACEA

***Bentheuphausia amblyops* (G. O. Sars)**

Thysanopoda (?) *amblyops* G. O. Sars 1884, Forh. Vidensk. Selsk., Christiania, (7):23.

Bentheuphausia amblyops G. O. Sars, 1885, Challenger Repts., Zool., 13 (37):109, pl. 19.

Specimens:

Hancock 2084-51, 2 immature females, 24 and 26 mm long; Hopkins, Tage 159B, 1 immature female, 12 mm long.

Distribution:

This bathypelagic species has never been reported from near Californian waters, although it has been collected off British Columbia (Banner, 1950) and in the eastern portion of the tropical Pacific (Hansen, 1912). Elsewhere it has been reported in the western tropical Pacific, the Indian, and the north and south Atlantic Oceans.

TABLE 4
RECORDS OF EUPHAUSID CAPTURES
HANCOCK FOUNDATION STATIONS

	<i>Bentheuphausia amblyops</i> (Sars)	<i>Nyctiphanes simplex</i> Hansen	<i>Euphausia eximia</i> Hansen	<i>Euphausia pacifica</i> Hansen	<i>Euphausia gibboides</i> Ortmann	<i>Thysanoessa spinifera</i> Holmes	<i>Thysanoessa gregaria</i> Sars	<i>Nematoscelis difficilis</i> Hansen	<i>Nematobrachion flexipes</i> (Ortmann)	<i>Stylocheiron maximum</i> Hansen	Euphausiid fragments
1663-49				1				3			
1861-49				1				About 90			
1863-49				5				4			
1864-49		12		2	2			16		1	Some
1866-49		12		9		4		3			
1867-49		2		37		2		13		1	
1906-49				16				About 100			
1934-50				2							
1991-50				5	2			12			
1994-50								1			
2008-51				22		4		8			
2009-51				1				1			
2037-51				About 1000		1		About 60			About 3
2048-51		2		About 2000-3000		5		About 140		10	About 3
2055-51				6				19			
2057-51				4	1			14			
2081-51		34	33					16	8	1	About 7
2084-51	2			2				7			
2135-52				About 60		3	1	About 130			

Remarks:

These specimens agree well with the original description of Sars with the exception of the outer uropod. According to the figure of Sars, the tip beyond the distal shoulder of the outer uropod is one-quarter the length of the entire ramus and is broadly rounded. In the smallest specimen the portion beyond the shoulder is only 0.15 the length of the branch and rounded. In the 24 mm specimen, on which only one uropod remains, the tip is less than 0.12 the length of the entire branch and the end is obliquely truncate. In the largest specimen the uropods are broken. The peculiar condition of the intact uropod of the 24 mm specimen may be due to chance disfiguration or it may be a basic difference, but it is more likely to be disfiguration.

The sex of the specimens was determined by the poor development of bristles at the base of antennular flagella, a character that was shown by Einarsson (1942) to be sexually dimorphic in this genus.³

Nyctiphanes simplex Hansen

Nyctiphanes simplex H. J. Hansen, 1911, Inst. Océanogr. Monaco, Bul., 210:20.

Nyctiphanes simplex H. J. Hansen, 1912, Mus. Comp. Zool. Harvard, Mem. 35(4):227, pl. 6, figs. 2a-2i, pl. 7, 1a-1b.

Specimens:

See Table 4.

Distribution:

The species has been reported previously from Californian waters by Esterly (1914). The species is known from the tropical and sub-tropical eastern Pacific, from 35° 31' N to 5° 57' S.

³ The strong development of these bristles definitely establishes the specimen reported from British Columbia (Banner, 1950), to be a male.

Euphausia Dana

Euphausia Dana, 1850, Am. J. Sci., II, 9:130.

In 1850 Dana described the genus *Euphausia* for four species of euphausiids (republished in 1852): *E. pellucida*, *E. superba*, *E. splendens*, and *E. gracilis*. The descriptions of the species were broad and did not mention many of the characteristics now considered to be important; the figures were small and lacking in detail. In 1885 Sars accepted and redescribed in detail what he considered to be these species. For a number of years the designations of Sars were accepted.

However, in a series of papers (1905b, 1910, 1911, and 1912) Hansen revised the entire classification of the genus, giving additional characteristics for the older species and describing many additional species. In these papers he discussed the species of Dana and their re-description by Sars. He pointed out that the type specimens of Dana were lost, so any interpretation would have to be placed upon his figures and descriptions alone. He stated:

"Dana's descriptions and figures of his four species of *Euphausia* are so imperfect that only one of his forms, viz. the gigantic Antarctic *E. superba*, can be recognized with any certainty. I am, however, able to prove that Sars' interpretations of the three other species, *E. pellucida*, *E. splendens* and *E. gracilis*, must be erroneous." (1905b, p. 8)

He then discussed the points in which Sars' specimens did not agree with the few points established by Dana.⁴ In conclusion, he cancelled the species of Dana as unrecognizable, and to Sars' recognizable species bearing Dana's names he gave new names.

Into this genus now have been placed some forty-five species, about thirty-six of which are accepted. However, of this thirty-six only one of the original names of Dana remains, and no subsequent worker has questioned the decision of Hansen.

Up to July, 1948, this procedure of Hansen was definitely against the International Rules of Zoological Nomenclature, and the names

⁴To Hansen's discussion of the differences between Sars' and Dana's *E. pellucida* should be added that Dana specifies: "First basal joint of inner antennae not produced at apex," yet Sars states: "Basal joint of antennulae with an erect leaflet above..."

applied by Hansen and others to new species were in jeopardy. Under the then current rules any person establishing again Dana's species (by neotype or otherwise) could have relegated to synonymy a name applied to the species after 1850.

However, the International Commission on Zoological Nomenclature at its July, 1948, session revised this rule with the approval of the Thirteenth International Congress of Zoology, first stating that zoologists were advised to follow the recommendations printed in the *Bulletin of Zoological Nomenclature* until the new *Règles* were printed (Bul. Zool. Nomen. 4(1-3):viii, 1950). As for the rule in question, they rescinded the old Article 31 (dealing with this subject) and stated (in part) that where the type material was lost, and where the specialists agreed that the taxonomic species could not be recognized, the name of the nominal species was to be treated as a *nomen dubium*, unavailable for future use. They also provided that if there were disagreement among the specialists, the question must be referred to the International Commission (*op. cit.* 4(4-6):74-76, 1950). (At the date of this writing it is impossible to determine officially whether this rule was again changed by the Fourteenth Congress in 1953.)

I propose, therefore, that this rule be applied to Hansen's action, and that the names *Euphausia pellucida* Dana, *E. superba* Dana, and *E. splendens* Dana be regarded henceforth as *nomina dubia*.

If any specialist on this group does not believe that Dana's species should be so regarded, I urge him to appeal to the International Commission, as called for in the citation above, as soon as possible so that the problem can be resolved permanently.

***Euphausia eximia* Hansen**

Euphausia eximia H. J. Hansen, 1911, Inst. Océanogr. Monaco, Bul., 210:23.

Euphausia eximia H. J. Hansen, 1912, Mus. Comp. Zool., Harvard, Mem., 35(4):230, pl. 7, figs. 2a-2g.

Specimens:

See Table 4.

Distribution:

This species is known only from the eastern tropical and subtropical Pacific, previous captures ranging from 26° N to $14\frac{1}{2}^{\circ}$ S. It seems to be more abundant in the central portion of that range. This record (at $27^{\circ} 29' 30''$ N) does not extend the known range.

Discussion:

This species is recognized easily by the combination of characteristics afforded by the lack of spines on the abdomen, the two lateral denticles on the margins of the carapace, and especially by the outstanding projection on the basal article of the antennular peduncle. These specimens agree perfectly with the descriptions and figures of Hansen, although the details of the first pleopods of the male were hard to ascertain because of the complex curves and expansions of the processes.

***Euphausia pacifica* Hansen**

Euphausia pacifica H. J. Hansen, 1911, Inst. Océanogr. Monaco, Bul., 210:28.

Euphausia pacifica, H. J. Hansen, 1915, U. S. Natl. Mus., Proc., 48:81, pl. 1, figs. 2a-2g.

Specimens:

See Table 4.

Distribution:

To judge from this collection, *E. pacifica* is one of the most common species in the waters off Southern California, as it is in the waters off Washington, British Columbia, and Alaska. Its range is known to extend from about 33° N. northward along the Pacific coast of North America to Alaskan waters and thence westward to the coast of Asia. It is found in both inshore and open ocean waters.

***Euphausia gibboides* Ortmann**

Euphausia gibboides Ortmann, 1893, Ergbn. Plankton-Exped., 2(G,b): 12, pl. 1, fig. 5.

Euphausia gibboides Hansen, 1912, Mus. Comp. Zool. Harvard, Mem., 35(4) : 252, pl. 9, figs. 2a-2h.

Euphausia gibba Esterly, 1914, U. Calif. Publ. Zool., 13(1) : 8.

Specimens:

See Table 4.

Distribution:

This species is quite well known from the tropical and subtropical Atlantic. In the Pacific it has been collected only in the tropical central and eastern portions. Ortmann (1894, p. 103) has recorded one collection of the species from near California ($35^{\circ} 19' 30''$ N., $125^{\circ} 21' 30''$ W.) However, it is likely that the specimens reported from La Jolla by Esterly as *E. gibba* Sars belong to this species (see below).

Discussion:

In the small collection of this species there is only one mature male, but on that the copulatory structures of the first pleopod agree perfectly with the descriptions and figures of Hansen (*loc. cit.*). However, there are differences in some of the other characteristics given for the species. The most notable difference is found in the rostrum, which was described and shown as a thin, laterally compressed structure arising abruptly from the low frontal plate, while in all of these specimens the rostrum is broader and arises as a direct continuation of the frontal triangle. The armature of the antennular peduncle is also different from the specimens described by Ortmann and Hansen, but this armature varies from one specimen to another. All specimens have a projecting lobe on the distal end of the basal article of the peduncle, but while in some this lobe continues as an acute tooth directed anterolaterally, in others it is directed almost anteriorly, and in a few young specimens the tooth is not developed at all. According to the plates of Hansen, the second article is supposed to project on the superodistal margin to form a low truncated lobe, but in many of the present specimens this lobe is longer than broad and rounded distally. The crest of the third article is like that described by Hansen in all except the smallest specimens. Finally Hansen described the lateral spine of the basicerite of the antennae as about half the length of the squame, while on these specimens it does not exceed one-third the length of that structure.

In view of the perfect comparison of the copulatory organs to those described for *E. gibboides*, and in view of the wide range of variation normally found in this group, these specimens were identified as *E. gibboides*.

Three of the twenty-two specimens from Hancock Station 2081-51 have been referred to this species with considerable doubts. None of the three are mature males and all are somewhat fragmentary. The antennular bases of the one specimen having them intact are like those described above; the other two look like they may have had a similar basal article. The form of the carapace and the general body form is the same as *E. gibboides*, but the third abdominal segment does not have any vestige of the posterior tooth characteristic of this species. It is possible that these belong to some species heretofore unreported from Californian or Mexican waters, but positive identification is impossible.

Esterly reported *Euphausia gibba* Sars from collections made at La Jolla, with some reservations. As he had no mature males, he could not confirm his identification with the structure of the copulatory organs. However, he did show in his figures and discuss in the text the structure of the antennular peduncle, which was of the same form as that described above, including the very characteristic tooth arising from the first article. For that reason his specimens have been placed in synonymy.

***Thysanoessa gregaria* G. O. Sars⁵**

Thysanoessa gregaria G. O. Sars, 1885, Challenger Repts. 13(37): 120, pl. 21, figs. 8-17, pl. 22.

Thysanoessa gregaria, H. J. Hansen, 1911, Inst. Océanogr. Monaco, Bul., 210:44 [description of the copulatory organ].

Specimens:

Hancock 2135-52, a mature male 10 mm long.

⁵The genus *Thysanoessa* was originally described with an "ö," but it was standard practice to ignore the umlaut in most English language journals until the Thirteenth International Congress of Zoology ruled that all diacritical marks were to be retained in scientific names. However, as I have heard that the Fourteenth International Congress in 1953 ruled contrariwise (the official proceedings are not yet available), I will omit the umlaut in this paper.

Distribution:

This species is known from north and south temperate Atlantic and from north and south temperate Pacific. Hansen (1915) also reported it from as far north in the Pacific as the Bering Sea, but I pointed out that this record was probably in error (1950). Another of Hansen's records was from off the Californian coast. The species was also recorded in Californian waters by Holmes (1900) and Esterly (1914).

Discussion:

The sole and rather battered specimen is not typical of the species, for the lateral denticle of the carapace is entirely lacking on one side and on the other it is reduced to a very slight indentation (really a "jog") of the margin. The thoracic legs are broken off, so their development could not be compared to the descriptions. Finally, on the copulatory organ of the first pleopod, the process P_2 has a concavity on the side towards process P_3 , a concavity not shown or discussed by Hansen.

***Thysanoessa spinifera* Holmes**

Thysanoessa spinifera Holmes, 1900, Calif. Acad. Sci., Occ. Papers, 7:229, pl. 4, fig. 81.

Specimens:

See Table 4.

Distribution:

The known range of this species is from off Southern California to the southeastern portion of the Bering Sea; in the northern portions of the range, at least, the species is abundant.

***Nematoscelis difficilis* Hansen**

Nematoscelis difficilis, H. J. Hansen, 1911, Inst. Océanogr. Monaco Bul., 210:48, fig. 18.

Nematoscelis megalops, Ortmann, 1894, (*nec. N. megalops* Sars, 1884 and 1885), Mus. Comp. Zool., Harvard, Bul., 25:103.

Nematoscelis microps Ortmann, 1894, (*partim*) (*loc. cit.*)

Specimens:

See Table 4.

Distribution:

This species has been recorded previously from Californian and northern Mexican waters by Hansen (1915) and Esterly (1914) and by me in the waters of Washington and British Columbia (1950). In this series of plankton tows it appears to be the most uniformly abundant species, although *Euphausia pacifica* Hansen occurs in greater swarms.

***Nematobranchion flexipes* (Ortmann)**

Stylocheiron flexipes Ortmann, 1893, Ergbn. Plankton-Exped. 2(G,b): 18, Taf. 1. fig. 7.

Nematodactylus flexipes Calman, 1896, R. Irish Acad., Trans., 31:16.

Nematobranchion flexipes Calman, 1905, Fish. Ireland Sci. Invest. for 1902-1903, 2(append. 4):153.

Specimens:

See Table 4.

Distribution:

This species is known from the north and south Atlantic, from the tropical eastern and western Pacific, from the north Pacific off Alaska, and from the Indian Ocean. This record, from off *Baja California*, is the first from Californian-Mexican waters.

Discussion:

In my 1950 paper I pointed out three characteristics in which the Alaskan specimens differed from the previous descriptions. These characteristics were the presence of lateral denticles on the carapace, a slightly more acute prerostral angle of the anterior carapace, and the presence of dorsal spinules on the sub-apical telsonal spines. The Mexican

specimens agree with the Alaskan specimens. It is likely that these differences are sufficient for the separation of this from the tropical species, but I do not believe it would be advisable to do so until specimens from the tropics are reexamined.

***Stylocheiron maximum* Hansen**

Stylocheiron maximum H. J. Hansen, 1908, Danish Ingolf Exped., 3(2):92.

Specimens:

See Table 4.

Distribution:

This species may have been present in the collection reported upon by Esterly in which he identified the specimens only to the genus (1914); otherwise it has not been reported from Californian waters. It is known to occur in the north and south Atlantic, in the Mediterranean Sea, in the Indian Ocean, and in the tropical Western Pacific; but the only reports from the eastern Pacific were those I made for the waters from Washington to Alaska (1950).

***Stylocheiron* sp.**

Several small specimens of possibly more than one species of *Stylocheiron* are found in the collections; however, their condition is so fragmentary, especially in the loss of the elongate legs, that specific identification is impossible. The most that can be said of them is that the form of their rostrums make it impossible for them to be *S. maximum* Hansen.

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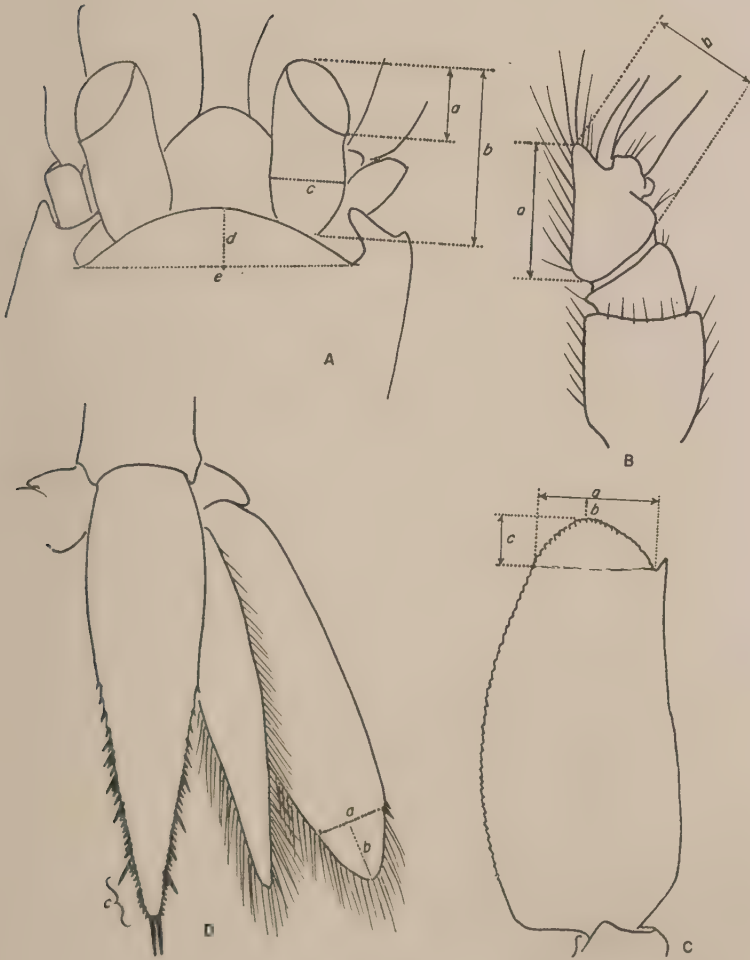
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BANNER

PLATE 1

Plate 1. Measurements used for *Eucopeia australis* Dana.

- A. Anterior carapace and eyes: *a*, cornea length; *b*, eye length; *c*, eye breadth; *d*, width of frontal plate; *e*, length of frontal plate.
- B. Antennular peduncle: *a*, breadth of distal article; *b*, length of distal article.
- C. Antennal squame; *a*, breadth of tip; *b*, the most distal point of tip, showing asymmetry; *c*, length of tip.
- D. Uropod and telson: *a*, breadth of tip of uropod; *b*, length of tip; *c*, small spines in last series.



AUSTROBILHARZIA VARIGLANDIS (MILLER AND NORTHUP, 1926)
PENNER, 1953, (TREMATODA: SCHISTOSOMATIDAE)
IN HAWAII WITH NOTES ON ITS BIOLOGY*

GEORGE W. T. C. CHU AND CHARLES E. CUTRESS

Department of Bacteriology and Department of Zoology,
University of Hawaii

INTRODUCTION

In November, 1950, apharyngeal, furcocercous cercariae were recovered from marine snails (*Littorina pintado* Wood) collected from the rocky shores of two bird islands just off the coast of Oahu in Hawaii. Chu (1952) reported the cercariae and the possibility of their being the etiological agent involved in local cases of "swimmers' itch." Subsequently, young noddy and sooty terns (*Anous stolidus pileatus* Scopoli and *Sterna fuscata oahuensis* Bloxam), chickens and ducks were experimentally exposed to these cercariae, and, as a result, sexually mature schistosomes were recovered from mesenteric veins in birds of all these species. All stages of the life cycle have been successfully maintained in the laboratory for more than 1 year. In December, 1952, adult worms identical with those raised experimentally were recovered from the mesenteric veins in 4 out of 8 ruddy turnstones, *Arenaria interpres interpres* (L.), killed on the island of Oahu. A careful comparison of the morphology of the adults and larval stages of the Hawaiian schistosome with that of other species in the subfamily SCHISTOSOMINAE, as far as published data have permitted, shows that the Hawaiian worm most closely resembles *Microbilharzia variglandis* (Miller and Northup, 1926) Stunkard and Hinchliffe, 1951.

However, the Hawaiian schistosome differs from *Microbilharzia chapini* Price, 1929, which Stunkard and Hinchliffe (1952) reduced to synonymy with *M. variglandis*. After comparing the description and figures of *M. variglandis* with the type of *M. chapini*,¹ it is hard to reconcile the striking difference between their ceca, which are straight and without diverticula in *M. chapini* but anastomosing and with numerous diverticula in *M. variglandis* (and in the Hawaiian schistosome). The configuration of this organ is so constant in the Hawaiian worms that it appears to rate consideration as a specific character. In addition, a comparison of cecal measurements for the 2 species, based on published descriptions (E. W. Price, 1929; Stunkard and Hinchliffe, 1952), shows that the common cecum of *M. chapini* is only about one-third the length of that in *M. variglandis*.

Penner (1953) suppressed the genus *Microbilharzia* and reallocated the species to the genus *Austrobilharzia* Johnston, 1916. He is probably correct in doing so, but such a change would be more justified had a rather complete morphological study of both the adult and larval stages of *Austrobilharzia terrigaleensis* been made.

Since rather complete reviews of the literature on the avian schistosomes have been included in several recent papers, *e. g.* Stunkard and Hinchliffe (1952), no

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review is included in this report. In view of the fact that several aspects of the adult and intermediate stages of *Austrobilharzia variglandis* have not been adequately described, the following additional observations on the morphology of the adults, the development of larval stages, as well as the mode of infection in both the definitive and intermediate hosts are offered.

THE ADULT STAGE

The adult Hawaiian schistosomes from both the ruddy turnstone and experimentally infected birds agree in most respects with the species described by Stunkard and Hinchliffe (1952). The dimensions of the more than 100 Hawaiian worms measured are, however, preponderantly greater than those recorded by these workers for their species. Our measurements were made from living worms after relaxation in a refrigerator, and from specimens compressed between cover glasses and fixed in Lavdowsky's fluid. One group of about 20 worms was measured before and after fixation, and it was found that the method employed in flattening our specimens so nearly compensated for any shrinkage during fixation that there was no appreciable difference in measurements of length and width between living and fixed worms. The few specimens that were observed to contract strongly or become contorted at the time of fixation were discarded. Since no obviously contracted or contorted worms were measured, we believe that the greater length and width of the Hawaiian species can be attributed largely to the condition of the specimens measured, although it may also be due, in part, to differences in their degree of maturity.

The sexually mature male Hawaiian worms (Fig. 1) measure 4.0–6.0 mm. by 0.28–0.56 mm. from natural infections and 4.0–7.0 mm. by 0.20–0.70 mm. from experimental infections. According to Stunkard and Hinchliffe, the Atlantic Coast species measures 2.94–4.22 mm. by 0.46 mm. In the Hawaiian species the gynae-cophoric canal begins at the oral sucker, and is lined with spines arranged in transverse bands about 13 microns wide separated by smooth areas of about 32 microns. The spines become much reduced in the preacetabular region. The canal cephalad of the acetabulum is very apparent in living specimens but indistinct in most preserved worms, which may account for Stunkard and Hinchliffe's placing the origin of the canal at the acetabulum of their worms. The fact that Stunkard and Hinchliffe (1952) figure the acetabulum to be within a Y-shaped "origin" of the canal strongly suggests that the canal actually does begin at the oral sucker in their specimens. If it originated at the acetabulum, the folds forming the canal would arise as an inverted V or as a line rather than as a Y. The number of testes varies with age. Spermatogenesis begins in the most posterior testis and gradually progresses cephalad as the more anterior primordia undergo organogenesis. Worms 2 weeks old generally possess 13 testes, those more than 4 weeks old average 20, and a few 4 months old have 23, the maximum number observed in Hawaiian worms. The excretory system in the male consists of 2 ventro-lateral protonephridia, whose main ducts arise just caudad of the oral sucker and unite just before the terminal excretory pore to form the definitive bladder. In the male (but not in the female) there is an accessory duct on each side which arises near the level of the beginning of the terminal cecum and joins the main duct a short distance cephalad of the definitive bladder. The flame cells occur binately in a bilateral

series, and most are lateral to the main protonephridial ducts. There are 4 lateral binary groups of flame cells along each accessory duct and 3 lateral and 2 medial binary groups along the terminal portion of each main duct. The capillaries from each binary group unite and in common join the ducts at rather constant intervals of about 50 microns. Not all the flame cells were visible in any one of the many worms examined, but those few flame cells obscured by other internal organs in 1 worm were seen clearly in one or more other specimens. The estimated number of flame cells for an average adult male (6 mm. long), based on direct observation and on calculations from their periodicity along the ducts, is approximately 280.

Sexually mature female schistosomes from Hawaii (Fig. 4), recovered from experimental infections, measure 3.0–7.0 mm. by 0.20–0.30 mm. in comparison with 2.0–3.5 mm. by 0.05–0.175 mm. recorded for female worms from the Atlantic Coast. Many authors dealing with schistosomes have regarded the number of eggs in the uterus as important. In mature females from Hawaii one egg is almost always found in the oötype, and a few worms have had 6 to 8 female germ cells scattered along the length of the long oviduct. However, only on rare occasions have eggs been found in the short uterus, which indicates that they probably pass through this organ rapidly. The excretory system of the female differs from that of the male in the more simple arrangement of the ducts in the region of the definitive bladder and in the shape of the bladder, which is trigonal in the female but cylindrical in the male. The protonephridial ducts arise immediately behind the oral sucker and unite posteriorly to form the definitive bladder. Most of the flame cells are lateral to the ducts, but occasionally some shift to a medial position. In the female the capillaries from the binary groups of flame cells unite and then join the ducts at about 85 micron intervals. The total number of flame cells in an average sized female (6 mm. long), estimated on the same bases as for the male, is approximately 164.

In all infected birds examined, the adult worms were usually recovered from the mesenteric veins adjacent to the ileum, but occasionally, in heavy experimental infections, a few worms were also taken from pancreatic veins and veins near the cloaca. On 2 occasions, involving repeatedly infected terns, 20 to 30 adult worms were recovered from veins in the liver. All natural infections were light, not more than 4 pairs of worms being recovered from 1 bird. Single and repeated infections of chickens and terns, although initiated by exposing the birds to more than 500 cercariae, have never yielded more than 60 males. However, in these infections polygamy was the rule, and 3 to 8 females occupied the gynaecophoric canal of most males. When many females occupied a gynaecophoric canal, some were small and retarded in development. On the contrary, bachelorhood in unisexual infections did not seem to alter the size of the male. Worms recovered from different species of birds exhibited no constant differences in size, morphology or rate of development.

EGGS

The eggs (Fig. 3) are slightly elliptical with a terminal spine which is usually bent as a "J" and is rarely straight or absent. Measurements of more than 50 eggs from fresh preparations are 75–140 microns by 67–126 microns, the preponderance being in the greater size range. The spine averages about 6 microns. There were no appreciable differences in size or shape of Hawaiian schistosome eggs recovered

from different species of birds or from old or young worms. Occasionally very small eggs were found, but these were obviously necrotic and should not confound the diagnosis.

The eggs in the feces of laboratory birds contained active, mature miracidia. Laboratory experiments revealed that the miracidia in the capsules died as soon as the feces dried, or, if the feces remained moist, the miracidia died within an hour, apparently from the toxic effects of the feces. In the light of these observations and the greater hazards to which schistosome eggs are subject on the "bird islands," it seems most likely that, if the miracidia are to hatch, the feces containing them must fall directly into sea water.

MIRACIDIA

Twenty-five living, fully- or nearly-extended miracidia (Fig. 2), hatched in a flask such as described by McMullen and Beaver (1945), measured 183–225 microns by 33–40 microns. The epidermis is uniformly covered with long cilia except for the lateral papillary line about one-fourth of the body length from the anterior end and the almost imperceptible interstices of the epidermal cells. The anterior fourth of the body is occupied by 2 elongate, unicellular penetration glands and a broad, multicellular apical gland (primitive gut), the latter containing coarse, eosinophilic granules. Immediately caudad of these glands is a large sac-like organ, sometimes called the "posterior penetrating gland" (Faust, 1949) or "central nerve mass" (Ameel, Van der Woude, and Cort, 1953; H. F. Price, 1931; and others). The organ, however, lacks many of the characteristics of either a gland or a ganglion (central nerve mass). In the miracidia of the Hawaiian worm it lies free in the parenchyma except at either end where a few filamentous strands connect it with the anterior glands and the posterior propagatory cells. Histologically it is made up of an outer, single layer of cuboidal cells and an inner, acellular, fibrous, slightly eosinophilic matrix. The cells are small with scant cytoplasm and with nuclei containing rather thick chromosomes. Consequently, the organ stains a deep purple with hematoxylin.

There is evidence of the organ in some developing miracidia while the latter are still within the capsules in the tissues of the definitive host. However, it is no longer apparent within a short time after the miracidium has penetrated the intermediate host. To learn the fate of this organ a group of *Littorina pintado* were infected with miracidia, and, after increasing intervals of time, the mantles containing the young mother sporocysts were cut off, fixed and sectioned. The slides made from these tissues revealed that the organ persisted without perceptible change until 4 hours after miracidial penetration. Between 4 and 12 hours the cells became dissociated, and beyond 12 hours after penetration the site of the organ contained only a loose aggregation of cells with pycnotic nuclei. These cells dispersed and decreased in number until, 48 hours after penetration, they were no longer recognizable.

Because of the transient nature of the organ, its total histological dissimilarity to nerve tissue, and evidence of mitosis in its cellular components, it seems doubtful that it is a ganglion. Likewise, because of the small size, scant cytoplasm and pycnotic nuclei of its cells, and the fibrous nature of the interior matrix, it does not resemble a gland. Further studies are in progress to more conclusively determine its nature.

In the posterior half of the body are 6 to 12 propagatory cells more or less enmeshed in a medial, filamentous stroma. The excretory system consists of 2 pairs of flame cells, the anterior pair lying lateral to the "central nerve mass," and the posterior pair located medial and caudad of the nephridiopore. The flame cell capillaries unite about one-third of the body length from the posterior and then descend to the lateral nephridiopore which opens about one-fourth the body length from the posterior end.

The miracidia freed themselves from the capsules by rotating violently until the end opposite the spine gave way. In fresh, clear sea water (they died quickly in water contaminated with feces) the miracidia were constantly-active, elongate organisms that assumed a pyriform shape only when they collided with obstacles or were in an adverse environment. When miracidia were placed with snails they exhibited no special ability to find the mollusc. However, once accidental contact was made with the snail, penetration always took place along the lateral margin of the mantle. In this location the miracidia transformed into mother sporocysts.

SPOROCYSTS

The morphology and development of schistosome sporocysts have been described in considerable detail by H. F. Price (1931), Cort and Olivier (1943), Cort, Ameel and Olivier (1944), and Cort, Ameel and Van der Woude (1953). There do not seem to be any basic morphological differences between the sporocysts of *Austrobilharzia variglandis* occurring in Hawaii and those of *Schistosomium douthitti* or *Trichobilharzia stagnicolae* as described by these workers.

Mother sporocysts removed from the mantle of *L. pintado* are translucent amorphous, sac-like organisms. Measurements of these sporocysts are not very significant because of their plasticity, but living ones measured 0.28–0.40 mm. by 0.12–0.14 mm. They attained their maximum size about 4 weeks after transformation from the miracidium and did not begin to decrease in size until after about 1 year. The first germ balls appeared at about 6 days, and their development into daughter sporocysts was rapid. The daughter sporocysts were first liberated between 30 and 40 days after miracidial penetration. They emerged from one end of the mother sporocyst through a protractile birth pore which had slightly lobulated margins. Mother sporocysts which were still liberating daughter sporocysts were recovered from the mantles of snails 1 year after infection. They seemed to have diminished in size and were opaque white due to an accumulation of oil droplets from fatty degeneration of most of the germ balls.

The daughter sporocysts of *A. variglandis* have already been described by Stunkard and Hinchliffe (1952). The measurements given for those of the Atlantic Coast are 0.654–1.38 mm. by 0.2–.392 mm. as compared to 0.63–0.84 mm. by 0.20–0.30 mm. for those of the Hawaiian worm. Little need be added to the existing description except that in the sporocysts from Hawaii an excretory system consisting of 4 pairs of flame cells was observed. The 4 flame cells on each side lie evenly spaced in the posterior half of the animal, with their capillaries uniting with the protonephridial duct near the anterior-most flame cell. The ducts then descend to the nephridiopore about one-fourth of the length of the sporocyst from the posterior end. It may be that 8 flame cells is not the total complement, but it was the greatest number that could be discerned in several favorable preparations.

After leaving the mother sporocysts, the daughter sporocysts migrate through

the tissues of the snail or possibly by way of the circulatory system, for they have on occasion been removed from the lumen of the snail's heart. Most of them become permanently entangled in the digestive gland of the snail, but in several heavy infections they were also found in the gonads. The daughter sporocysts first shed cercariae at about 4 months, and after 1 year were still shedding them without the slightest sign of abatement.

CERCARIAE

The cercariae of the Hawaiian *A. variglandis* are morphologically indistinguishable from those described and figured by Stunkard and Hinchliffe except for slight discrepancies in dimensions. The measurements in millimeters for body length, body width, tail stem length, furcal length, and acetabular diameter are 0.248, 0.091, 0.202, 0.108, and 0.028, respectively, for the Hawaiian form as compared with 0.237, 0.072, 0.228, 0.126, and 0.023 for the Atlantic Coast form. The cercariae from both the Atlantic Coast and Hawaii were first fixed in 10% hot formalin. Stunkard and Hinchliffe's figures represent averages of 10 specimens whereas those from Hawaii are averages of 50 specimens.

In Hawaii the *Littorina pintado* carrying infections of *A. variglandis* are found on water-covered sea benches of two "bird islands" (Moku Manu and Manana). In these areas about 1% of the snails are infected, with little or no seasonal fluctuation. In spite of the fact that *L. pintado* snails are very numerous in these areas and that flocks of sooty and noddy terns and golden plover (*Pluvialis dominica fulva* (Gmelin)) are frequently observed on the flats, not one of 40 terns and 12 golden plover collected on these benches were infected with *A. variglandis*. However, most people who have collected on these benches have, at one time or another, experienced cercarial dermatitis.

MODE OF INFECTION

In the laboratory natural emergence of cercariae from infected snails was always light even after the snails had been dried for several days before immersion. Consequently, all infections of laboratory animals were made by cracking snails and utilizing the "top swimming" cercariae. Liberated cercariae in fresh sea water gradually lost their ability to penetrate and generally died in about 18 to 24 hours when kept at room temperature. Refrigeration prolonged their life for periods up to 6 or 7 days, but the cercariae had then lost all their ability to penetrate. In 0.85% saline, at room temperature, they remained alive and normal in appearance for about 14 hours.

To preclude the possibility of naturally acquired helminthic infections in experimental definitive hosts, all domestic birds used were raised from newly-hatched stock and the terns, from downy young. Infection of the experimental birds was readily achieved by introducing cercariae into the eyes or cloacae or by immersing their feet in sea water containing cercariae. The cercariae usually penetrated in about 15 minutes. On only a few occasions did a noticeable dermatitis occur on the feet or tarsi of these birds. After cercarial penetration, the young worms reached the lungs in 3 days at which time they measured from 0.3 to 0.5 mm. in length.

Cercarial penetration in rats and man usually resulted in a mild dermatitis. Slides made from sectioned skin with cercarial lesions, taken from the abdomens

of 8 young rats, revealed that the penetrated cercariae lodged in both the dermis and subdermis and that the cercariae in the lesions were recognizable up to 4 days. The sections through the lesions showed a pronounced infiltration of eosinophils and lymphocytes to the immediate area. Two mice whose tails were exposed to cercariae, when killed and examined 4 and 5 days later, were found to have hemorrhagic areas and plasma-filled vesicles on their lungs. When the lungs were sectioned these areas were found to be heavily infiltrated with leucocytes, but no parasites were observed. It appeared that lung migration had occurred, but that the worms had already undergone lysis. Ability of this marine avian schistosome to reach the mammalian lungs appeared to be similar to that observed for fresh water avian schistosomes as reported by Olivier (1953).

The growth of *A. variglandis* in the lungs of terns or chickens was rapid, and by the sixth day, when most of the worms migrated to the mesenteric veins, they were already 1 to 2 mm. long. But after repeated infections it was observed that the young worms lingered in the lungs from 9 to 10 days and attained sizes up to 3 mm.

Observations based on autopsies of over 40 birds (terns, ducks and chickens) which had been subjected to either single or repeated infections indicated that migration of the worms to the mesenteric veins was direct and rapid. At the time of migration worms were usually found in either the pulmonary veins or mesenteric veins or in both but rarely elsewhere. On 2 occasions, however, worms probably in the act of migration were recovered from the chambers of the heart and the aortic arch. And, on 2 other occasions involving terns that had been repeatedly infected, 20 to 30 worms were recovered from the veins of the liver, and many eggs were present in the venules. The mesenteric veins of 1 tern contained an additional 20 worms but in the other bird no worms occurred in these vessels.

As soon as the worms reached the mesenteric veins the females entered the gynaecophoric canals of the males and 5 or 6 days thereafter were shedding eggs. Egg production by the female was always observed to be light.

Development of the sporocysts has already been mentioned but is here repeated, in part, for continuity. In the natural intermediate host (*Littorina pintado*), miracidia of *A. variglandis* were found to have penetrated the lateral margin of the mantle and there metamorphosed into mother sporocysts which remained in this location throughout the course of infection. Daughter sporocysts were first liberated between 30 and 40 days after miracidial penetration and migrated through the tissues of the snail to the digestive gland where they became enmeshed in the stroma of that organ. Cercariae were first shed about 4 months after infection of the snail, and such infections persisted for more than a year.

The natural definitive host (*Arenaria interpres interpres*) of *A. variglandis* in the Islands is a winter resident, arriving in September and usually departing in May. They are common throughout the Islands during that period, but only a few non-nesting individuals remain in the summer. Species of birds from the "bird islands," examined for schistosomes but found negative, are *Puffinus pacificus cuneatus* Salvin, *Pluvialis dominica fulva* (Gmelin), *Anous stolidus pileatus* Scopoli and *Sterna fuscata oahuensis* Bloxam.

In nature *L. pintado* are presumably infected by bird droppings containing the schistosome eggs which fall directly into the shallow water covering the snails. Three species of *Littorina* (*L. picta*, *L. undulata* and *L. pintado*) occur on the sea

benches of both Moku Manu and Manana Islands, but sporocysts have been found only in *L. pintado*. None of the several other species of operculate gastropods occurring in the same area [*Thais intermedia* (Diener), *T. harpa* (Conrad), *Drupa ricinus* (L.) and *Morula brunneolabrum* Dall] were ever found infected with larval schistosomes, nor were any of them capable of being experimentally infected. *Littorina scabra*, a fourth littorine species found in Hawaii, is a large form that spends most of its time above water in bay areas. Although examinations of over 5,000 *L. scabra* from various localities were negative for all types of trematode infection, snails of this species were infected experimentally with *A. variglandis* miracidia and yielded cercariae on cracking.

Two other trematodes utilize *L. pintado* on the "bird islands" as an intermediate host. Approximately 50% of these snails were infected with larval stages of *Parorchis acanthus* (Nicoll) and about 0.01% contained an undetermined, minute cercaria. Occasionally *L. pintado* snails were found with mixed infections of both *A. variglandis* and *P. acanthus*.

SUMMARY

The larval schistosome inhabiting the marine snail *Littorina pintado* Wood (previously reported from Hawaii) has now been identified as that of *Austrobilharzia variglandis* (Miller and Northup, 1926) Penner, 1953. In the natural definitive host, *Arenaria interpres interpres* (L.), adult worms were recovered from the mesenteric veins.

Experimentally, chickens, ducks, noddy terns and sooty terns were successfully infected with the cercariae of this schistosome. Although 4 species of littorine snails occur in Hawaii, only *L. pintado* was found to be a natural intermediate host. In the laboratory, however, *L. scabra* proved infectable with miracidia of *A. variglandis*.

A few morphological details of the adults and larvae of *A. variglandis*, not previously reported, are presented. In addition the mode of infection in both the intermediate and definitive hosts, as observed in the laboratory, are given.

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EXPLANATION OF FIGURES

FIG. 1. Male, *A. variglandis*, semi-diagrammatic composite drawing showing the general arrangement of the internal organs, especially the excretory system.

FIG. 2. Miracidium, *A. variglandis*, drawn from a photomicrograph of a living miracidium.

FIG. 3. Egg, *A. variglandis*, drawn from a photomicrograph of a living encapsulated miracidium isolated from feces of infected terns.

FIG. 4. Female, *A. variglandis*, semi-diagrammatic composite drawing, somewhat broader in proportion to its length in comparison with the natural appearance of a living or fixed specimen.

PLATE I

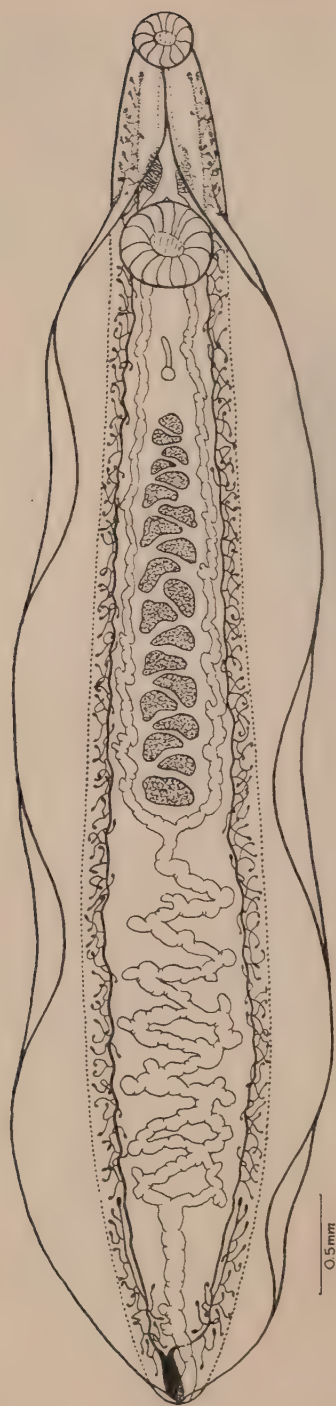


Fig. 1

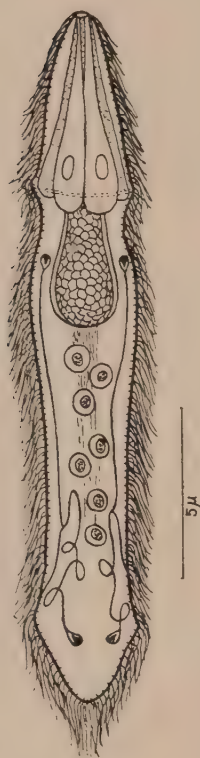


Fig. 2

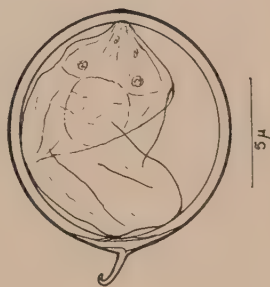


Fig. 3



Fig. 4

